

CANOPY STRUCTURE, LIGHT PENETRATION AND TREE GROWTH AT
DIFFERENT CONFIGURATIONS IN VARIOUS 18-YEAR-OLD SLASH PINE
(Pinus elliottii Engelm. var. elliottii) STANDS IN FLORIDA

BY

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I dedicate this dissertation to my parents, José A. Sequeira Ortega and Emelina Vindas Vindas, whose infinite love and support have always inspired me, and to my brothers and sister.

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A study was conducted for a 2-yr period in an 18 to 19-yr-old slash pine (Pinus elliotii Engelm. var. elliottii)/native understory silvopastoral system in central Florida. The main objective was to determine the effect of spacing configuration (single vs double rows) at constant stand density on canopy structure, light penetration and tree growth. Below-canopy photosynthetically active radiation (PAR) and soil temperature were monitored along transects within plots to determine annual, seasonal and daily patterns of variation. Above-canopy PAR was continuously recorded as reference during sampling periods. Stem and crown dimensions were measured and growth rates estimated on trees adjacent to transects. A destructive sampling was carried out to determine leaf biomass and leaf area index (LAI).

Crown area and crown depth were positively correlated ($R^2 = 0.64$), and each was also positively correlated to stem volume ($R^2 = 0.83$ and 0.70 , respectively) in all the stands. On the other hand, crown area ($R^2 = 0.62$) and stem volume ($R^2 = 0.90$) were negatively correlated to light penetration (above-canopy:below-canopy PAR ratio). Crown depth and light penetration were weakly correlated and no trend was observed. Soil temperature and light penetration were positively correlated ($R^2 = 0.61$) in all the configurations. Overall, single-row stands had greater crown area by 27%, and biomass and LAI of new foliage by 32% and 30%, respectively, than double-row stands. This was reflected in higher annual canopy light interception (60% more), stem volume (55% more) and growth rates (63% more) for the control stand than for the double-row stand at the closest within-row spacing. Conversely, the latter allowed more light penetration (by 48%) to the understory. Differences in annual, seasonal and daily light penetration and extinction coefficient (k) and soil temperature were observed between single-row and double-row configurations.

These findings could be used in canopy geometry models to optimize both tree and understory productivity by simulating light penetration at wide-row spacings. Such models could have great potential for the improvement of silvopastoral systems as widely practiced in southeastern U.S. and many tropical regions.

CHAPTER 1 INTRODUCTION

Forest productivity has been related to canopy light interception (Linder 1985), and there is great current interest worldwide in providing further tests of this apparent relationship. If established, this would have a great impact on the development of management practices for manipulation of stand structure to optimize both tree and understory growth in silvopastoral systems (Grace 1987). However, the influence of stand geometry on individual tree crown architecture and on this type of relationship remains a major uncertainty (Oker-Blom 1985).

Stand geometry can be manipulated either by changing stand density (number of trees/unit ground area) or spacing configuration (spatial distribution of trees at a given density, including orientation of rows). Silvopastoral systems are a type of agroforestry in which trees and pastures are grown together to optimize both tree fiber and animal production (Nair 1985). Stand geometry should play a vital role in such systems regulating aboveground competition for sunlight among trees and between trees and understory vegetation. Tree arrangement could be used effectively to manipulate canopy structure and, therefore, the relative

amounts of light available through and under the tree canopies. Effect of stand configuration on tree growth, forage and cattle yields has been studied for a number of years in pine-pasture silvopastoral systems in central Florida. Nevertheless, the problem of how competition for light among trees and between trees and understory vegetation may affect both wood and forage production has not yet been properly addressed. Research in pine stands planted at conventional close spacings, e.g., 2.4x3.6 m, has consistently shown that forage yields, although initially high, dropped rapidly after about 10 yrs when canopy closure occurs (e.g., Lewis 1989). It has been suggested, therefore, that forage production could be potentially enhanced by planting trees closer together in widely spaced rows without seriously affecting wood yields.

In 1970, the U.S. Forest Service established a field experiment consisting of slash pine (Pinus elliotii Engelm. var. elliotii) planted at single-row and double-row spacing configurations at the same stand density to test this hypothesis. Although preliminary measurements at age 13 yrs (Lewis et al. 1985b) showed only slight differences in tree growth among spacing configurations, it was expected that these differences would become more significant with increasing time. In addition, the study at 13 yrs did not include an analysis of the bio-ecological factors which may lead to differences in tree growth among the configurations.

My study, which involved field research over a 2-yr

period, utilized the existing experiment to evaluate the productive potential of this agroforestry system between ages 18 and 19 yrs.

Objectives

The overall objective was to determine the effect of spacing configuration on canopy structure, direct sunlight penetration and tree growth in a 18-19-yr-old slash pine plantation in north-central Florida. Specifically, I set out to:

1. determine the effect of different spacing configurations (single-row vs double-row spacings) on canopy structure (crown depth, area, volume and ratio), foliar biomass (old and new foliage and twigs), leaf area index (LAI) and leaf area density at a constant stand density,
2. determine the effect of canopy structure, foliar biomass and LAI on direct sunlight penetration (relative amounts of light available to the trees and understory vegetation), canopy light extinction characteristics, soil temperature and stem growth, and
3. determine daily, seasonal and annual patterns of variation in the above-canopy to below-canopy PAR ratio (direct sunlight penetration) and soil temperature and their relationship to spacing configuration, canopy structure, leaf biomass and LAI.

Working Hypotheses

Hypothesis 1. More crowded trees (i.e., wider spacings between rows and closer spacings within rows) have smaller crowns, foliar biomasses and leaf areas than more widely spaced trees.

Hypothesis 2. As a result, and also due to greater competition for sunlight between and within adjacent tree rows, stem dimensions and growth in double-row stands are lower than in single-row stands. However, suppressed tree growth could be offset by higher direct sunlight penetration per unit ground area to potential understory vegetation through larger canopy gaps between the double rows.

Hypothesis 3. Daily, seasonal and annual variations in direct sunlight penetration and soil temperature occur among spacing configurations related to changes in canopy structure and the solar radiation flux and angle. Double-row stands have significantly greater direct sunlight penetration and soil temperature at all times due to less developed canopy covers than single-row stands.

CHAPTER 2 LITERATURE REVIEW

Several studies provide evidence of a close relationship between canopy structure, light penetration and tree growth. For instance, annual intercepted PAR and annual canopy photosynthesis decreased at closer within-row spacings in a Pinus radiata D. Don silvopastoral system in New Zealand (38°9'S, 176°16'E) at 100 stems/ha (Grace 1987). Although yearly canopy photosynthesis was only slightly higher in north-south oriented rows, yearly intercepted PAR was about 10% higher than in east-west oriented rows. If a linear relation is assumed between aboveground dry matter production and intercepted PAR, then both tree spacing and row orientation should affect the overall productivity of these stands. In this case, tree spacing appeared to have a greater impact than row orientation on tree growth, although this may be an artifact of the low tree densities used.

Changes in stand structure may lead to differences in canopy architecture that are closely associated with stemwood production. Nevertheless, research in the past has often disregarded variability in the horizontal or vertical distribution of leaf area within the canopy and potential correlations between canopy architecture and the conversion

rate of solar radiation to stemwood. Using tree height (m) as an indicator of both stand age and site quality, but one relatively insensitive to stand density, stemwood growth (volume increment per unit ground area per m height, $\text{m}^3/\text{ha}/\text{m}$) of Pinus contorta Douglas var. latifolia Engel. (Critch.) stands was found to be dependent on the amount and vertical distribution of leaf area (foliar density, m^2/m^3) within the canopy (Smith and Long 1989). In this case, high stand "vigor" (resistance to pests and pathogens) was related to deep full crowns and fast individual tree growth. However, high stand stemwood production ($\text{m}^3/\text{ha}/\text{yr}$) and growth efficiency (stemwood production per m per unit LAI, $\text{m}^3/\text{m}/\text{m}^2$) were associated with short, compact crowns and moderate individual tree growth.

Modeling of canopy architecture has shown that optimal productivity is achieved by maximizing light capture while minimizing irradiance variation on needle surfaces. For instance, greater light interception and photosynthetic rate at low sun angles and high latitudes have been obtained with narrow-crowned stands (Pukkala and Kuuluvainen 1987). On the other hand, greater productivity at high sun elevations was obtained from broad-crowned stands. Given equal interception, photosynthetic efficiency (net photosynthesis per unit light intercepted) was greater for broader crowns.

Shade tolerance of tree species can also have a crucial effect on crown architecture, light interception and

photosynthetic rates. Thus, in a simulation study of successional development patterns in a Pinus sylvestris L. (shade-intolerant)/Picea abies (L.) Karst (shade-tolerant) stand, light penetration to the lower canopy fell below the compensation point for Pinus over time, raising its canopy base height above that of Picea (Leemans and Prentice 1987). The lower compensation point of Picea allowed maximum LAI and leaf area per tree and foliage per unit basal area twice as much as for Pinus, which gradually lost its lower branches.

Stand composition and canopy architecture also can have a large influence on the stand light environment and spectral quality. Photosynthetic photon flux density (PPFD) values and percent of daily PPFD totals recorded for a tropical moist deciduous forest were 5 to 10 times larger than those for humid tropical forests, due to a seasonally more open canopy which allowed a greater penetration of less spectrally altered sunlight (Lee 1989). Seasonal variation in LAI did not have a significant effect on light penetration through the canopy of mature slash pine plantations, probably due to their highly aggregated canopy structure (Gholz et al. 1991). Maximum annual LAI (all-sided) varied 20% over a 3-yr period, with values ranging from 3.0 to 6.5 and repeated fertilization increasing maximum LAI by more than 40%. Mean annual light penetration through the canopy was 31%, with an 18% to 42% seasonal variation. The high response of annual aboveground net primary productivity (ANPP) to fertilizer was related to

the nutritional influence on LAI. Annual and seasonal variation in LAI was reasonably predicted through a model of needle litterfall incorporating basal area and climatic conditions from the spring of the previous year.

Changes in understory aboveground biomass of Douglas-fir (Pseudotsuga menziessii (Mirb.) Franco.) stands with age have been closely associated with changes in canopy structure (Long and Turner 1975). Foliage biomass, total crown and total tree weight all increased with age, whereas total understory declined. An equilibrium crown and foliage weight (8.5 to 9.0×10^3 kg/ha) was reached earlier in a plantation (after 36 yrs) than in a natural stand (after 60 yrs) due to faster biomass increments promoted by the higher stand density and earlier crown closure in the plantation.

All of the above studies point out the close association between canopy structure, light penetration and overstory-understory productivity. My study, therefore, was basically aimed at determining this relationship as affected by stand configuration in an agroforestry context in Florida.

CHAPTER 3 MATERIALS AND METHODS

Study Site

Field trials for my study were established in early 1970 on the eastern portion of the Richloam Unit of the Withlacoochee State Forest near Brooksville, north-central Florida (Shepherd and Lennartz 1970) (Fig. 1). The study area was located on a slash pine flatwoods site with an estimated site index (age 50 yrs) of 21 m. Soils of the area belong to the Myakka-Immokalee-Waveland association (south Sumter County) and can be classified as sandy, siliceous, hyperthermic, Aeric or Arenic Haplaquods (i.e., nearly level, poorly drained, sandy soils, with a dark sandy subsoil, and soils with a cemented sandy subsoil; Caldwell and Johnson 1982). Native vegetation of the site was typical of wet pine flatwoods, with slash (*Pinus elliotii* Engelm. var. *elliotii*) and longleaf (*P. palustris* Mill) pines as dominant overstory species, and saw-palmetto (*Serenoa repens* (Bartr.) Small), gallberry (*Ilex glabra* (L.) A. Gray) and pineland three-awn (*Aristida stricta* Michx.) dominating the understory (Lewis et al. 1985b).

The study site was located approximately at 28°40'N latitude and 82°05'W longitude and at 22.5 m elevation. Mean



Fig. 1. Location of study site at the Withlacoochee State Forest, Sumter County, central Florida. Latitude: $28^{\circ}40'N$, longitude: $82^{\circ}05'W$. Elevation: 22.5 m.

total annual rainfall (1951-1980) in the area is 1305.8 mm, with normal annual temperatures (1951-1980) of 14.8 (min.), 21.4 (mean) and 28.1 (max.) °C (NOAA 1983a). Mean possible annual sunshine is 65% to 70% (2800-3000 hrs), with a mean annual daily solar radiation of 18.84 to 20.93 MJ/m² and a mean annual sky cover from sunrise to sunset of 5 to 6 tenths (10 = complete sky coverage) (NOAA 1983b).

Site preparation in 1969 included clear-cutting (stems only removed), double-chopping of residues and broadcast burning. The area was never mowed, thinned or fertilized. A prescribed burn of the understory vegetation occurred in 1982, and light cattle grazing was allowed during the first five years.

Experimental Design and Statistical Analysis

Spacing Configurations

Trees were planted in 1970 at six spacing configurations and a constant stand density of 1122 trees/ha (Fig. 2). The experimental layout consisted of a completely randomized design with six treatments and two replications (i.e., 12 plots). Whole-plot area was 1.2 ha (120*100 m), with an internal measurement plot of 0.36 ha (60*60 m).

Non-Destructive Tree Measurements and Data Analysis

In order to determine canopy structure, stem dimensions and growth rates of slash pine under different configurations,

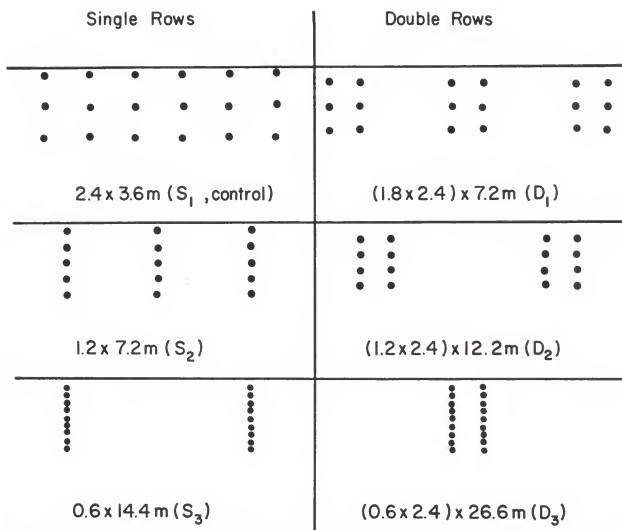


Fig. 2. Spacing configurations of the various study plots. The constant planting density was 1122 trees/ha (after Shepherd and Lennartz 1970).

a non-destructive tree measurement was carried out. Two random transects per plot were established for a total of 24 transects. All transects ran perpendicular to tree rows, with a 3-tree minimal distance between transects and plot edges or significant gaps in the stand. Transect ends were marked with polyvinyl chloride (PVC) poles half-way between either two adjacent single rows or two adjacent double rows (Fig. 3) and flagged at 1-m intervals.

Six trees per transect (three on each side of the transect) were selected in the single-row plots (72 trees), and 12 trees per transect (six on each side of the transect) in the double-row plots (144 trees), for a total sample of 206 trees (five trees from single-row and five from double-row configurations were unavoidably missing). Tree height (h , m) was measured with a clinometer (Suunto) and diameter at breast height (dbh, cm) measured 1.3 m above ground level with a cloth tape between March and May 1988. These data were compared to those reported at age 13 yrs by Lewis et al. (1985b).

The following formulas were applied to estimate stem dimensions and growth rates (assuming 100% tree survival):

$$\text{basal area (m}^2\text{/ha)} = \pi * r^2, \quad (1)$$

where r = stem radius,

$$\text{stem volume (m}^3\text{/ha)} = 0.0399 + 0.002645 * \text{dbh}^2 * h, \quad (2)$$

(Moehring et al. 1973),

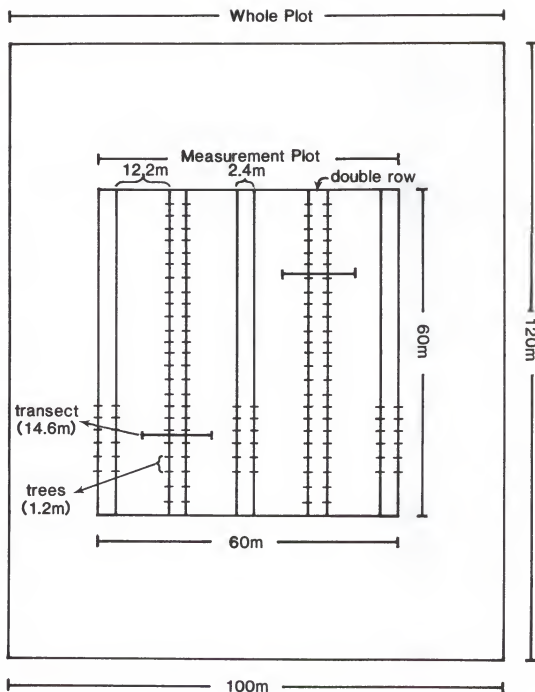


Fig. 3. Example of sampling design in a double-row configuration. Spacing is $(1.2 \times 2.4) \times 12.2\text{m}$.

$$\text{basal area increment (m}^2\text{/ha/yr)} = (\text{ba18} - \text{ba13})/5, \quad (3)$$

where ba18 and ba13 are basal areas at 18 and 13 yrs, respectively,

$$\begin{aligned} \text{stem volume increment (m}^3\text{/ha/yr)} = \\ (\text{vol18} - \text{vol13})/5, \end{aligned} \quad (4)$$

where vol18 and vol13 are stem volumes at 18 and 13 yrs, respectively.

Also, height to the base of the live crown (lch, m) and crown radius (crd, m) were measured for each tree in four directions (N-E-S-W, along and perpendicular to the N-S- oriented rows) to estimate crown parameters according to the following formulas:

$$\text{Crown area (m}^2\text{)} = \pi * \text{crd}^2, \quad (5)$$

$$\text{Crown depth (m)} = h - \text{lch}, \quad (6)$$

$$\text{Crown volume (m}^3\text{)} = \text{ca} * \text{cd} / 3, \quad (7)$$

$$\text{Crown ratio} = \text{cd} / h. \quad (8)$$

Analysis of variance (ANOVA) was performed using the General Linear Models Procedure (GLM) of the Statistical Analysis System (SAS) Program (Freund and Littell 1981) in order to determine the sources of variation in the experimental data. The following model was applied:

$$\text{mx} = \text{config} + \text{rep}(\text{config}), \quad (9)$$

where mx = variable mean by transect per replication per configuration, config = effect of configuration, and rep(config) = effect of replication within configuration.

Significance levels (p) varied from 0.04 to 0.0001 for the range of ANOVAs evaluated. Once it was established by the ANOVA analyses that all variables were significantly affected by spacing configuration, means comparisons were carried out using the Dunnett's t ($\alpha \leq 0.10$). In addition, the following orthogonal contrasts were tested ($\alpha \leq 0.10$) (Freund and Littell 1981): double vs single rows, i.e., the mean of $D_1 + D_2 + D_3$ vs the mean of $S_1 + S_2 + S_3$, D_1 vs the mean of $D_2 + D_3$, D_2 vs D_3 , S_1 vs the mean of $S_2 + S_3$, and S_2 vs S_3 . The number of contrasts was limited by the degrees of freedom ($n - 1 = 5$). Linear regression analysis of canopy structure and stem dimensions was also conducted using Sigma-Plot version 3.0 (Jandel Corp. 1986).

Destructive Sampling and Data Analysis

In order to determine whether leaf biomass and leaf area were related to the crown geometries as assessed above at different stand configurations, a destructive sampling of a subsample of trees from four configurations was conducted between October 2 and 6, 1989. Randomly selected, healthy trees (10 per configuration, for a total sample of 40 trees) were cut from S_1 (control plot), S_3 , D_1 , and D_3 . These four configurations were selected on the basis of their being representative of the range of experimental variability among configurations.

In addition to total height, dbh, crown radius and height to the base of the live crown for comparison with the non-destructive data, leaf area (m^2) and leaf biomass (kg) were measured on each tree. First, each tree was debranched, the foliar clumps cut off and total foliage and twig fresh weight (kg) determined. Then a 10% sample of the total foliage and twig biomass from each tree was weighed fresh in the field. Total dry weights of old and new foliage (Wf) and twigs (Wt) were estimated as follows:

$$Wf \text{ (kg)} = (f/s) * tot, \quad (10)$$

where f = dry weight of needles in the sample (corrected for 55% of water content, Gholz and Fisher 1982), s = fresh weight of sample (leaders excluded), and tot = fresh weight of total foliage and twig biomass (leaders included).

$$Wt \text{ (kg)} = (t/s) * tot, \quad (11)$$

where t = dry weight of twigs in the sample (corrected for 49% water content, Gholz and Fisher 1982).

A subsample of 10 fascicles/tree was then taken from this sample to measure length (cm), fresh and oven-dry weight (g) of needles (water volume displacement technique). Specific leaf area (sLA , all-sided) was then estimated through the following formula (Johnson 1984):

$$sLA \text{ (cm}^2\text{/g)} = [2 * l * (1 + (\pi/n)) * (v/(\pi * l))^2] / w, \quad (12)$$

where l = cumulative length of needles in the subsample, n = number of needles per fascicle, v = needles' volume, and w =

needles' dry weight. Finally, LAI (all-sided) and leaf area density (LAd) were calculated as follows:

$$\text{LAI (m}^2\text{/m}^2\text{)} = \text{sLA} * \text{Wf} / 10000, \quad (13)$$

$$\text{LAd (m}^2\text{/m}^3\text{)} = \text{LAI} / \text{crown depth}. \quad (14)$$

The SAS GLM procedure was used to perform the ANOVA applying the following model:

$$x = \text{config}, \quad (15)$$

where x = variable value for each individual tree and config = effect of configuration. Significance levels (p) ranged from 0.05 to 0.0001. As all the ANOVAs were significant at $p \leq 0.05$, comparisons of the mean values for the four configurations used were then conducted using the Dunnett's t ($\alpha \leq 0.05$). The following non-orthogonal contrasts were also evaluated ($\alpha \leq 0.05$) (Freund and Littell 1981): double vs single rows, i.e., the mean of $D_1 + D_3$ vs the mean of $S_1 + S_3$, D_1 vs D_3 , and D_3 vs S_3 . The number of contrasts corresponded to the degrees of freedom ($n - 1 = 3$). Linear regression analysis of leaf biomass and leaf area was also performed using Sigma-Plot version 3.0 (Jandel Corp. 1986).

Light Penetration, Soil Temperature and Data Analysis

Diurnal, seasonal and annual variations in direct photosynthetically active radiation (PAR: 0.4-0.7/ μm) and soil temperature ($^{\circ}\text{C}$) were considered in this study. Below-canopy PAR (bPAR, $\mu\text{mol/m}^2\text{/s}$) under mostly clear sky conditions was read once a month with a LiCor line quantum sensor (1 m long)

connected to an integrating quantum radiometer/photometer (LI-188B), using a 10-sec integrating time, at 1 m above ground level and at 1-m intervals along the transects. Soil temperature (at 5 cm depth) was read simultaneous with the below-canopy PAR measurements and at the same transect locations.

On each sampling day, six 1-hr time intervals were first designated for both below-canopy PAR and soil temperature readings. Randomly selected plots were then monitored between 10:00 and 16:00 hrs E.S.T. (at about 30 min/plot); monthly measurements were made in all 12 plots each month. Above-canopy PAR (aPAR, $\mu\text{mol}/\text{m}^2/\text{s}$) was continuously recorded using a 1-min integrating time, with a LiCor spot quantum sensor (LI-190SB) mounted on a 10-m aluminum pole set up in the open and connected to an Omnidata Polycorder 516-B. Mean hourly above-canopy PAR values were calculated for the entire sampling period and canopy light penetration then defined as:

$$\text{PAR ratio} = \text{bPAR}/\text{aPAR}. \quad (16)$$

Light penetration and soil temperature data were analyzed as a balanced incomplete block design using the SAS GLM procedure. The following model was applied for the ANOVA:

$$\begin{aligned} \text{mx} = & \text{config} + \text{season} + \text{month}(\text{season}) + \text{season} \times \text{config} + \\ & \text{time} + \text{season} \times \text{time} + \text{config} \times \text{time}, \end{aligned} \quad (17)$$

where mx = variable means for each configuration per measurement time, config = effect of configuration, season = effect of season, month(season) = effect of month within

season, seasonxconfig = effect of the season by configuration interaction, time = effect of time of day, seasonxtime = effect of the season by time interaction, and configxtime = effect of the config by time interaction. Significance values (p) ranged from 0.002 to 0.0001, and means comparisons were then performed using Dunnett's t ($\alpha \leq 0.05$). Also, the following contrasts were tested ($\alpha \leq 0.05$) (Freund and Littell 1981): double vs single rows, i.e., the mean of $D_1 + D_2 + D_3$ vs the mean of $S_1 + S_2 + S_3$, D_1 vs the mean of $D_2 + D_3$, D_2 vs D_3 , S_1 vs the mean of $S_2 + S_3$, and S_2 vs S_3 (orthogonal); winter vs spring, winter vs summer, summer vs fall, and spring vs fall (non-orthogonal). The number of contrasts was restricted by the degrees of freedom in the case of orthogonal ($n - 1 = 5$), but not for non-orthogonal contrasts ($n - 1 = 3$). Linear regression analysis of the data was also conducted using Sigma-Plot version 3.0 (Jandel Corp. 1986) in order to relate canopy structure to light penetration and soil temperature.

Following a similar field sampling methodology, four diurnal PAR measurements were carried out under mostly clear sky conditions, with readings made between 08:00 and 16:00 hrs E.S.T. in three of the configurations (S_1 , D_2 and D_3).

In order to relate canopy structure to light extinction coefficients, k values for each diurnal and configuration were calculated according to Lambert-Beer's law as follows:

$$k = -\log(\text{PAR ratio})/((\cos \alpha) * \text{LAI}), \quad (18)$$

where α = zenith angle at reading time. Measured LAI values

(October 1989) were adjusted according to the seasonal patterns reported by Gholz et al. (1991) for slash pine stands in north Florida to provide estimates for the diurnal dates: LAI = 5.19 (30 November 1988), 4.66 (27 January 1989), 4.92 (23 June 1989), and 4.06 (26 February 1990). Likewise, seasonal LAIs (mean annual = 5.00) were estimated as 3-month averages as follows: LAI = 4.46 (winter), 4.26 (spring), 5.21 (summer), and 6.07 (fall). In this case, α angle was not taken into consideration.

The diurnal data were analyzed using the SAS GLM procedure and, in this case, the model applied for the ANOVA was as follows:

$$mx = \text{config} + \text{time}, \quad (19)$$

where mx = variable means for each configuration per measurement time, config = effect of configuration, and time = effect of time of day. Significance levels (p) ranged from 0.05 to 0.0001. Means comparisons were then conducted by testing the following orthogonal contrasts ($\alpha \leq 0.05$) (Freund and Littell 1981): double v_s single rows, i.e., the mean of $D_2 + D_3$ v_s the control, and D_2 v_s D_3 . The number of contrasts was determined by the degrees of freedom ($n - 1 = 2$).

CHAPTER 4 RESULTS

Non-Destructive Tree Dimensional Sampling

In this section, data from the non-destructive tree dimensional sampling are analyzed. I will focus on the effect of spacing configuration on canopy structure, stem dimensions and growth rates, as well as, the relationship between canopy structure and stem dimensions.

Canopy Structure and Spacing Configuration

Crown area among configurations (Table 1) ranged from 11.5 (S_1) to 5.5 m² (D_3). Single-row stands had 27% greater average crown area than double-row stands based on the orthogonal contrasts ($\alpha \leq 0.05$). Also, configurations S_3 , D_2 and D_3 had smaller crown areas than the control (S_1). For both single-row and double-row stands, crown area tended to decrease at closer within-row spacings and wider between-row spacings.

Crown depth (Table 1) varied only within a narrow range, from 5.7 (S_3) to 4.8 m (D_3), and no differences were detected among configurations. Again, the average of single-row stands tended to be larger than for double-row stands. For single-row stands, crown depth tended to decrease at wider within-row

spacings and closer between-row spacings, whereas double-row stands tended to have an opposite trend.

Table 1. Mean crown characteristics of 18-yr-old slash pine stands at different spacing configurations, Withlacoochee State Forest (n = 24 trees for single-row stands, n = 48 trees for double-row stands).

Spacing config ^a	Crown area (m ²)	Crown depth (cd, m)	Crown volume (m ³)	Crown ratio (cd:h)
S ₁	11.5(6.5)	5.0(2.0)	21.5(17.3)	0.34(0.13)
S ₂	9.3(3.9)	5.5(1.5)	17.9(10.2)	0.37(0.08)
S ₃	8.1(4.4)*	5.7(1.4)	16.4(11.2)	0.40(0.07)*
D ₁	8.6(3.5)	5.2(1.2)	15.6(9.0)	0.37(0.06)
D ₂	6.9(3.1)*	5.1(1.2)	12.4(8.0)*	0.35(0.06)
D ₃	5.5(2.7)*	4.8(1.5)	9.6(7.6)*	0.38(0.08)

^aS₁: 2.4x3.6 m, S₂: 1.2x7.2 m, S₃: 0.6x14.4 m, D₁: (1.8x2.4)x7.2 m, D₂: (1.2x2.4)x12.2 m, D₃: (0.6x2.4)x26.6 m.

*Means significantly different from the control (S₁) by Dunnett's t test ($\alpha \leq 0.10$). Numbers in parentheses denote standard deviations.

Crown volume (Table 1) varied by 55% over the configurations, but only D₂ and D₃ were significantly smaller than S₁. As with crown area, crown volume tended to decrease at closer within-row, but wider between-row spacings, for all the stands. Crown ratio (Table 1) ranged from 0.40 (S₃) to 0.34 (S₁), but with only S₃ significantly larger (6%) than S₁. For single-row stands, crown ratio tended to decrease at wider within-row, but closer between-row spacings; there was no trend for double-row stands.

Stem Dimensions and Growth Rates in Relation to Spacing Configuration

The control stands had larger dbh than all the other configurations, over the range of 18.3 (S_1) to 12.3 cm (D_3) (Table 2). Also, differences in dbh were found between the average of $S_2 + S_3$ and the control, and between the average of $D_2 + D_3$ and D_1 (with larger dbh for the second of each of the paired configurations) based on orthogonal contrasts ($\alpha \leq 0.05$). Single-row stands tended to have greater average dbh than double-row stands. For both single-row and double-row stands, dbh decreased at closer within-row and wider between-row spacings.

Table 2. Mean stem dimensions of 18-yr-old slash pine stands at different spacing configurations, Withlacoochee State Forest (n = 24 trees for single-row stands, n = 48 trees for double-row stands).

Spacing config ^a	Dbh (cm)	Height (h, m)	Basal area ^b (m ² /ha)	Volume ^b (m ³ /ha)
S_1	18.3(3.9)	13.9(2.4)	30.8(12.4)	220.4(112.4)
S_2	16.6(2.9)*	14.6(1.5)	25.0(8.3)*	183.4(71.4)
S_3	14.3(3.2)*	14.2(1.9)	18.8(9.2)*	138.8(86.6)*
D_1	16.8(3.0)*	14.3(2.0)	25.6(9.2)*	184.7(82.8)
D_2	14.8(3.2)*	14.5(1.6)	20.1(9.0)*	148.0(77.6)*
D_3	12.3(3.4)*	12.7(2.5)*	14.4(8.6)*	98.4(82.1)*

^a S_1 : 2.4x3.6 m, S_2 : 1.2x7.2 m, S_3 : 0.6x14.4 m, D_1 : (1.8x2.4)x7.2 m, D_2 : (1.2x2.4)x12.2 m, D_3 : (0.6x2.4)x26.6 m.

^b100% tree survival assumed.

*Means significantly different from the control (S_1) by Dunnett's t test ($\alpha \leq 0.10$). Numbers in parentheses denote standard deviations.

Tree height had only a 13% range, from 14.6 (S_2) to 12.7 m (D_3), and only D_3 was significantly different from the control (Table 2); besides trees tending to be taller in both single-row and double-row stands at intermediate spacings, other trends were not apparent.

Mean basal area differences followed a pattern similar to that for dbh, but with clearer trends across spacings (Table 2). Basal area had a 53% range, from 30.8 (S_1) to 14.4 m²/ha (D_3). Each configuration was lower in basal area compared to the control, and so was the average of $S_2 + S_3$ based on orthogonal contrasts ($\alpha \leq 0.05$).

Mean stem volume, a function of both dbh and height, ranged over 55%, from 220.4 (S_1) to 98.4 m³/ha (D_3). Configurations S_3 , D_2 and D_3 had lower stem volume than the control (Table 2). As with basal area, average stem volume of single-row stands was comparable to double-row stands. Stem volume followed the same overall trends as dbh and basal area across spacings.

Growth rates were estimated by comparing stem dimensions at ages 13 yrs (Lewis et al. 1985b) and 18 yrs (Table 3). Basal area and stem volume increments decreased at closer within-row and wider between-row spacings for all the stands. On average, growth rates were greater for single-row than for double-row stands; values ranged from 3.84 (S_1) to 1.30 (D_2) m²/ha/yr for basal area, and from 31.44 (S_1) to 11.56 (D_3) m³/ha/yr for stem volume.

Table 3. Mean annual growth rates of slash pine stands between ages 13 and 18 yrs at different spacing configurations, Withlacoochee State Forest.

Spacing config ^a	ba13 ^b ---(m ² /ha)---	ba18 ^c (m ² /ha/yr)	ba1 ^d (m ² /ha/yr)	vol13 ^e ---(m ³ /ha)---	vol18 ^f (m ³ /ha/yr)	vol1 ^g (m ³ /ha/yr)
S ₁	11.6	30.8	3.84	63.2	220.4	31.44
S ₂	11.2	25.0*	2.76	60.6	183.4	24.56
S ₃	12.0	18.8*	1.36	68.1	138.8*	14.14
D ₁	9.1*	25.6*	3.30	46.0*	184.7	27.74
D ₂	13.6	20.1*	1.30	76.0	148.0*	14.40
D ₃	7.6*	14.4*	1.36	40.6*	98.4*	11.56

^aS₁: 2.4x3.6 m, S₂: 1.2x7.2 m, S₃: 0.6x14.4 m, D₁: (1.8x2.4)x7.2 m, D₂: (1.2x2.4)x12.2 m, D₃: (0.6x2.4)x26.6 m.

^{b,c,d}Basal area at ages 13 and 18 yrs, and basal area increment, respectively.

^{e,f,g}Stem volume at ages 13 and 18 yrs, and stem volume increment, respectively.

*Means significantly different from the control (S₁) by Dunnett's test ($\alpha \leq 0.10$).

Relationships between Canopy Structure and Stem Dimension Variables

In order to assess effect of canopy structure on stem dimensions, linear regression analysis of the data was carried out. This showed a positive correlation between crown depth (m) and crown area (m²) for both single-row ($R^2 = 0.42$) and double-row ($R^2 = 0.64$) stands (Fig. 4). The two crown depth outlying points for single-row stands correspond to transects in one of the control plots. Since there were no differences in crown depth means among configurations, this can be ascribed to random variation.

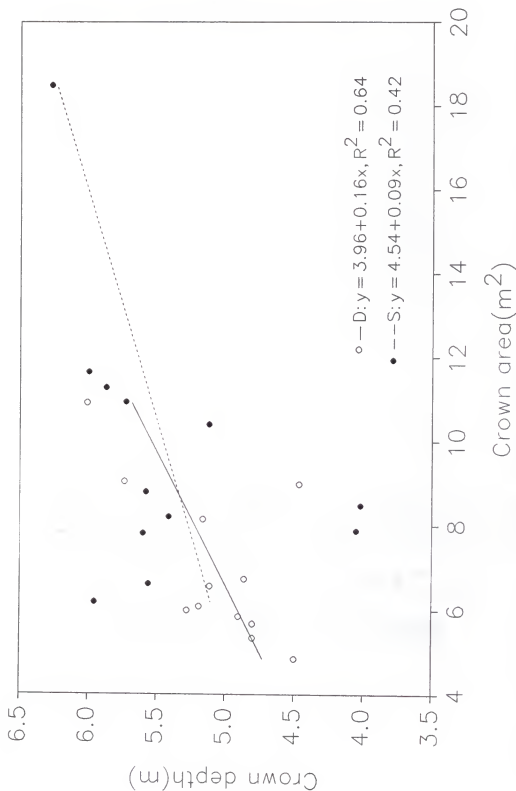


Fig. 4. Regressions of crown depth on crown area of 18-yr-old slash pine at single-row (S) vs double-row (D) configurations (n = 12 transects).

Double-row stands showed more consistent values. Stem volume (m^3) increased similarly with increasing crown area for both single-row ($R^2 = 0.83$) and double-row ($R^2 = 0.57$) stands (Fig. 5). Likewise, stem volume and crown depth were positively correlated for both single-row ($R^2 = 0.45$) and double-row ($R^2 = 0.70$) stands (Fig. 6). Crown area and depth and stem volume values were smaller and remained within a narrower range for double-row as compared to single-row configurations. Therefore, except for the relationship between stem volume and crown area, higher slopes and closer correlations were obtained for double-row than for single-row stands. However, the relationships were similar for both configurations.

Destructive Tree Sampling

Leaf Biomass in Relation to Stem Dimensions and Spacing Configuration

Linear regression analysis of biomass data for individual trees (Table 4) in this case had greater R^2 values than other non-linear relationships (quadratic, logarithmic) tested. In general, leaf and twig biomass tended to increase with increasing dbh for all the stands, this trend being more evident for new than for old biomass. Dry weight of old foliage tended to increase at increasing dbh (cm) and wider within-row (but closer between-row) spacings for all the stands. When separated by configuration, higher correlations between weight of old foliage and dbh were found for S_3 and D_1 .

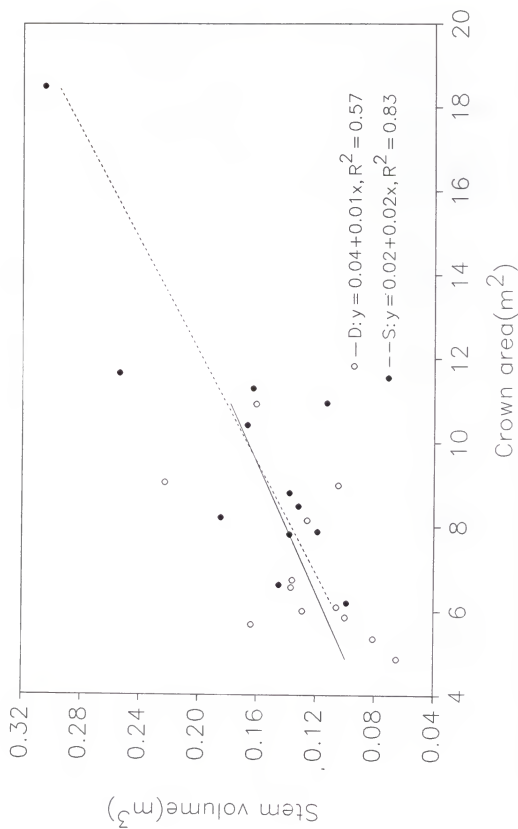


Fig. 5. Regressions of stem volume on crown area of 18-yr-old slash pine at single-row (S) vs double-row (D) configurations ($n = 12$ transects).

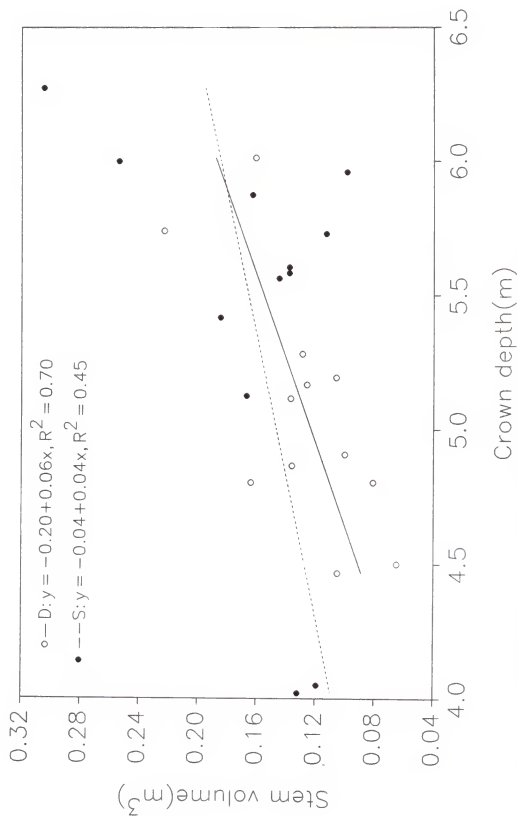


Fig. 6. Regressions of stem volume on crown depth of 18-yr-old slash pine at single-row (S) vs double-row (D) configurations ($n = 12$ transects).

Table 4. Statistics of significant ($p \leq 0.10$) regressions based on a 10-tree destructive sampling from each of four configurations, Withlacoochee State Forest. Statistics are also provided for the pooled data sets.

$y = a + bx$, where $x = \text{dbh (cm)}$ and $y = \text{leaf biomass (kg)/tree}$.					
Component(y)	Config ^a	a	b	R ²	p
Old Foliage	S ₁	----	----	----	ns
	S ₃	-7.63	0.59	0.71	0.02
	D ₁	-12.20	0.91	0.62	0.05
	D ₃	----	----	----	ns
	pooled	-1.56	0.25	0.48	<0.01
New Foliage	S ₁	-9.27	0.75	0.83	<0.01
	S ₃	-12.53	1.05	0.84	<0.01
	D ₁	----	----	----	ns
	D ₃	----	----	----	ns
	pooled	-5.47	0.60	0.75	<0.01
Old Twigs	S ₁	----	----	----	ns
	S ₃	-2.64	0.23	0.68	0.03
	D ₁	----	----	----	ns
	D ₃	----	----	----	ns
	pooled	-0.77	0.12	0.45	<0.01
New Twigs	S ₁	-1.80	0.16	0.76	0.01
	S ₃	-2.01	0.19	0.76	0.01
	D ₁	----	----	----	ns
	D ₃	-0.53	0.08	0.74	0.02
	pooled	-1.27	0.14	0.76	<0.01

^aS₁: 2.4x3.6 m, S₃: 0.6x14.4 m, D₁: (1.8x2.4)x7.2 m, D₃: (0.6x2.4)x26.6 m.

A better correlation was obtained between dry weight of new foliage and dbh. The analysis by configuration indicated closer correlations between weight of new foliage and dbh for S_3 and S_1 .

Regression analysis for individual trees also revealed a linear relationship between old twig biomass and dbh. When split by configuration, a higher correlation between old twig biomass and dbh was found only for S_3 . On the other hand, new twig biomass and dbh were better correlated. Further analysis by configuration showed close correlations between new twig biomass and dbh for S_1 , S_3 and D_3 .

No differences in mean weight of old foliage were found among configurations; S_1 tended to have the greatest (3.30 kg/tree) and D_3 the smallest weights (1.99 kg/tree) (Table 5). The double-row stand at the widest within-row spacing (D_1) tended to have a larger weight of old foliage (3.17 kg) than the single-row stand (S_3) at the closest within-row spacing (2.67 kg). On the other hand, differences in weight of new foliage were observed between D_3 and the control (S_1), and between D_3 and S_3 (with larger values for the second of each of the paired configurations) based on the non-orthogonal contrasts ($\alpha \leq 0.05$). Also, average weight of new foliage was 32% greater for single-row than for double-row stands. The largest mean corresponded to S_1 (6.38 kg/tree) and the smallest to D_3 (3.42 kg/tree); S_3 and D_1 were not significantly different.

Table 5. Mean canopy biomass (old and new foliage and twigs) of 19-yr-old slash pine stands at different spacing configurations, Withlacoochee State Forest (n = 10 trees per configuration).

Spacing config ^a	Wof ^b	Wnf ^c	Wot ^d	Wnt ^e
	(dry weight, kg/tree)			
S ₁	3.30(1.49)	6.38(2.47)	1.56(0.70)	1.45(0.56)
S ₃	2.67(1.76)	5.68(2.65)	1.37(0.72)	1.21(0.51)
D ₁	3.17(1.69)	4.79(1.91)	1.30(1.06)	1.05(0.43)
D ₃	1.99(0.50)	3.42(1.00)*	0.95(0.38)	0.68(0.20)*

^aS₁: 2.4x3.6 m, S₂: 1.2x7.2 m, S₃: 0.6x14.4 m, D₁: (1.8x2.4)x7.2 m, D₂: (1.2x2.4)x12.2 m, D₃: (0.6x2.4)x26.6 m.

^b,^cWeight of old and new foliage, respectively.

^d,^eWeight of old and new twigs, respectively.

*Means significantly different from the control (S₁) by Dunnett's t test ($\alpha \leq 0.05$). Numbers in parentheses denote standard deviations.

There were no differences in weight of old twigs among configurations, although S₁ tended to have a larger value (1.56 kg/tree) than D₃ (0.95 kg/tree). On the other hand, differences in weight of new twigs between D₃ and S₁, and between D₃ and S₃ were significant (with larger values for the second of each of the paired configurations) based on non-orthogonal contrasts ($\alpha \leq 0.05$), with the greatest (S₁) 53% larger than the smallest (D₃). Also, the average value was 35% greater for single-row than for double-row stands. For all the stands, weight of new twigs decreased at closer within-row and wider between-row spacings, i.e., S₁ > S₃ > D₁ > D₃. In this respect, it behaved in a similar way as old and new foliage and old twigs.

Leaf Area in Relation to Spacing Configuration and Canopy Structure

There were no differences in mean specific leaf area of old foliage among the configurations (Table 6), which ranged from 71.00 (D_3) to 68.39 (S_1) cm^2/g .

Table 6. Mean specific leaf area (old and new foliage) of 19-yr-old slash pine stands at different spacing configurations, Withlacoochee State Forest ($n = 10$ trees per configuration).

Spacing config ^a	sLAO ^b ----- (cm^2/g)	sLAN ^c -----
S_1	68.39(4.77)*	79.16(5.19)
S_3	68.48(2.97)	78.44(2.82)
D_1	69.76(4.10)	80.08(4.10)
D_3	71.00(3.64)	81.97(3.38)

^a S_1 : 2.4x3.6 m, S_3 : 0.6x14.4 m, D_1 : (1.8x2.4)x7.2 m, D_3 : (0.6x2.4)x26.6 m.

^{b,c}Specific leaf area of old and new foliage, respectively.

*Numbers in parentheses denote standard deviations.

Specific leaf areas of new foliage varied by only 4%, from 81.97 (D_3) to 78.44 (S_3) cm^2/g . The LAI of old foliage of S_1 (2.53) tended to be the largest, whereas that of D_3 (1.57) the smallest (Table 7). On the other hand, LAI of new foliage of D_3 was smaller than those of S_1 and S_3 , and the average of double-row configurations was 30% smaller than that of single-row configurations based on non-orthogonal contrasts ($\alpha \leq 0.05$). The largest LAI of new foliage corresponded to S_1 (5.60) and the smallest to D_3 (3.13). Also, S_3 tended to have

Table 7. Mean leaf area index (old and new foliage and total) and leaf area density of 19-yr-old slash pine stands at different spacing configurations, Withlacoochee State Forest (n = 10 trees per configuration).

Spacing config ^a	LAIo ^b -----	LAI _n ^c (m ² /m ²) -----	LAI _t ^d -----	LAd ^e (m ² /m ³)
S ₁	2.53(1.17)	5.60(2.04)	8.13(2.80)	1.14(0.37)
S ₃	2.03(1.27)	4.96(2.15)	6.99(3.32)	1.07(0.44)
D ₁	2.46(1.28)	4.30(1.73)	6.76(2.90)	1.06(0.42)
D ₃	1.57(0.38)	3.13(0.87)*	4.70(1.17)*	0.93(0.28)

^aS₁: 2.4x3.6 m, S₃: 0.6x14.4 m, D₁: (1.8x2.4)x7.2 m, D₃: (0.6x2.4)x26.6 m.

^b, ^c, ^dLeaf area index (all-sided) of old, new and total foliage, respectively.

^eLeaf area density.

*Means significantly different from the control (S₁) by Dunnett's t test ($\alpha \leq 0.05$). Numbers in parentheses denote standard deviations.

a greater mean value than the D₁ configuration. Total LAI, the sum of LAI of old and new foliage, was also smaller for D₃ as compared to S₁, and averaged 24% more for double-row than for single-row configurations based on the non-orthogonal contrasts ($\alpha \leq 0.05$). Total LAI ranged over 42%, from 8.13 (S₁) to 4.70 (D₃), with an overall mean of 6.65 ± 2.55 . Leaf area density values ranged from 1.14 (S₁) to 0.93 m²/m³ (D₃), but no differences were found among configurations. It also tended to decrease at closer within-row (but wider between-row) spacings for all the stands (S₁ > S₃ > D₁ > D₃).

In order to determine the relationship between leaf area and crown structure, linear regression analysis for individual trees was performed (Table 8). This revealed that leaf area

Table 8. Statistics of significant ($p \leq 0.10$) regressions based on a 10-tree destructive sampling from each of four configurations, Withlacoochee State Forest. Statistics are also provided for the pooled data sets.

A. $y = a + bx$, where $x = \text{crown area (m}^2\text{)}$ and $y = \text{leaf area (m}^2\text{)}/\text{tree}$.					
Component(y)	Config ^a	a	b	R ²	p
Old foliage	pooled	11.04	0.81	0.41	<0.01
New foliage	S ₁	21.52	1.96	0.57	0.09
	S ₃	----	----	----	ns
	D ₁	11.32	2.94	0.62	0.06
	D ₃	----	----	----	ns
	pooled	20.17	1.99	0.58	<0.01
Total	pooled	31.21	2.80	0.55	<0.01
B. $y = a + bx$, where $x = \text{crown volume (m}^3\text{)}$ and $y = \text{leaf area (m}^2\text{)}/\text{tree}$.					
Component(y)	Config ^a	a	b	R ²	p
Old foliage	pooled	13.14	0.27	0.40	0.01
New foliage	S ₁	23.53	0.74	0.66	0.04
	S ₃	----	----	----	ns
	D ₁	18.33	1.00	0.59	0.07
	D ₃	----	----	----	ns
	pooled	24.56	0.69	0.60	<0.01
Total	S ₁	37.04	1.00	0.64	0.04
	S ₃	----	----	----	ns
	D ₁	27.52	1.64	0.57	0.08
	D ₃	----	----	----	ns
	pooled	37.70	0.95	0.56	<0.01

^aS₁: 2.4x3.6 m, S₃: 0.6x14.4 m, D₁: (1.8x2.4)x7.2 m, D₃: (0.6x2.4)x26.6 m.

of old foliage (m^2/tree) tended to increase at increasing crown area and crown volume. An even better correlation was found between these two crown parameters and leaf area of new foliage (m^2/tree). Somewhat closer correlations between leaf area of new foliage and crown area were obtained for D_1 , and between leaf area of new foliage and crown volume for S_1 . As expected, a fairly good correlation was also found between total leaf area (m^2/tree), and crown area and crown volume, with a better correlation between total leaf area and crown volume obtained for S_1 .

The general trend in this case was for leaf area to increase with increasing crown area and crown volume for both single-row and double-row configurations. However, the closer fits were obtained between new and total leaf area and crown volume.

Light Penetration and Soil Temperature

Annual Light Penetration, Soil Temperature and Spacing Configuration

No differences in above-canopy PAR among treatments were observed; mean values ranged from 1260 (S_2) to 1204 (D_3) $\mu\text{mol}/\text{m}^2/\text{s}$ throughout the year (Table 9). On the other hand, configurations D_3 and S_3 had higher below-canopy PAR than the control. Likewise, the paired configurations of D_1 and $D_2 + D_3$ (i.e., the average of D_2 and D_3), D_2 and D_3 , and S_1 and $S_2 + S_3$, were all different (lower values for the first of each of the paired configurations) based on orthogonal contrasts ($\alpha \leq$

Table 9. Mean annual light conditions and soil temperature in 18-yr-old slash pine stands at different spacing configurations, Withlacoochee State Forest.

Spacing config ^a	aPAR ^b --($\mu\text{mol}/\text{m}^2/\text{s}$)--	bPAR ^c	PAR ratio (bPAR:aPAR)	k ^d (LAI ^e =5.00)	Soil temp (°C)
S ₁	1236(315)	364(220)	0.30(0.19)	0.40(0.18)	20.6(4.4)
S ₂	1260(318)	474(249)	0.37(0.17)	0.34(0.20)	21.0(4.7)
S ₃	1210(330)	554(240)*	0.45(0.14)*	0.28(0.10)	21.1(4.4)
D ₁	1247(323)	389(154)	0.31(0.10)	0.38(0.13)	20.7(4.5)
D ₂	1257(265)	492(207)	0.39(0.13)	0.32(0.14)	21.4(4.9)*
D ₃	1204(367)	701(237)*	0.58(0.11)*	0.22(0.09)*	21.3(4.5)*

^aS₁: 2.4x3.6 m, S₂: 1.2x7.2 m, S₃: 0.6x14.4 m, D₁: (1.8x2.4)x7.2 m, D₂: (1.2x2.4)x12.2 m, D₃: (0.6x2.4)x26.6 m.

^{b,c}Above-canopy and below-canopy photosynthetically active radiation, respectively.

^dLight extinction coefficient.

^eLeaf area index (all-sided).

*Means significantly different from the control (S₁) by Dunnett's t test ($\alpha \leq 0.05$). Numbers in parentheses indicate standard deviations.

0.05). The greatest value (701 $\mu\text{mol}/\text{m}^2/\text{s}$) corresponded to the double-row stand at the widest spacing between rows (D₃) and the smallest (364 $\mu\text{mol}/\text{m}^2/\text{s}$) to the single-row stand at the closest spacing between rows (control). For all the stands, below-canopy PAR decreased at wider within-row and closer between-row spacings. However, average below-canopy PARs of single-row and double-row stands were similar.

The maximum fractional light penetration (below-canopy:above-canopy PAR ratio) (0.58, D₃) was almost double the minimum (0.30, S₁). However, on the average, double-row

stands were no different than single-row stands. For both single-row and double-row stands, the PAR ratio tended to decrease at wider within-row and closer between-row spacings (e.g., S_3 was greater than S_1 , and D_3 tended to be greater than D_1).

The pattern was the opposite for the light extinction coefficient (k) at a mean LAI of 5.00, which ranged from 0.40 (S_1) to 0.22 (D_3). Again, average values for single-row and double-row stands were similar. There was a trend for k to decrease at closer within-row and wider between-row spacings for all the stands. Differences were found between S_1 and D_3 , D_2 and D_3 , D_1 and $D_2 + D_3$, and S_1 and $S_2 + S_3$ (with higher k for the first of each of the paired configurations) based on orthogonal contrasts ($\alpha \leq 0.05$).

Mean annual soil temperature had a narrow range of only 4%, from 21.4 (D_2) to 20.6 (S_1) °C, with no significant differences between double-row and single-row stands (Table 9). There were differences between the control and both D_2 and D_3 , between D_1 and $D_2 + D_3$, and between S_1 and $S_2 + S_3$ (with lower soil temperature for the first of each of the paired configurations) based on orthogonal contrasts ($\alpha \leq 0.05$). As with light penetration and below-canopy PAR, soil temperature tended to decrease at wider within-row and closer between-row spacings for both single-row and double-row stands.

Annual Light Penetration and Soil Temperature in Relation to Canopy Structure and Stem Dimensions

There was a fairly good linear correlation between annual light penetration and crown area (m^2), with PAR ratio decreasing at increasing crown area for both single-row ($R^2 = 0.32$) and double-row ($R^2 = 0.62$) stands. The slope of the curve was much less for single-row than for double-row stands (Fig. 7). Light penetration varied with crown depth (m), but it tended to increase linearly with crown depth for single-row stands ($R^2 = 0.42$), while decreasing at increasing crown depth for double-row stands ($R^2 = 0.52$) (Fig. 8). The apparently contrasting response in single-row stands was probably a result of greater variability among trees sampled and, hence, may not be an effect of stand geometry.

Similarly, a negative relationship was observed between stem volume (m^3) and PAR ratio, with both single-row ($R^2 = 0.44$) and double-row ($R^2 = 0.90$) volumes decreasing linearly with increasing PAR ratio (Fig. 9).

Regression analysis indicated a positive linear relationship between soil temperature and light penetration for single-row ($R^2 = 0.61$) and double-row ($R^2 = 0.37$) stands (Fig. 10). In both cases, soil temperature seemed constant at PAR ratios over 0.45.

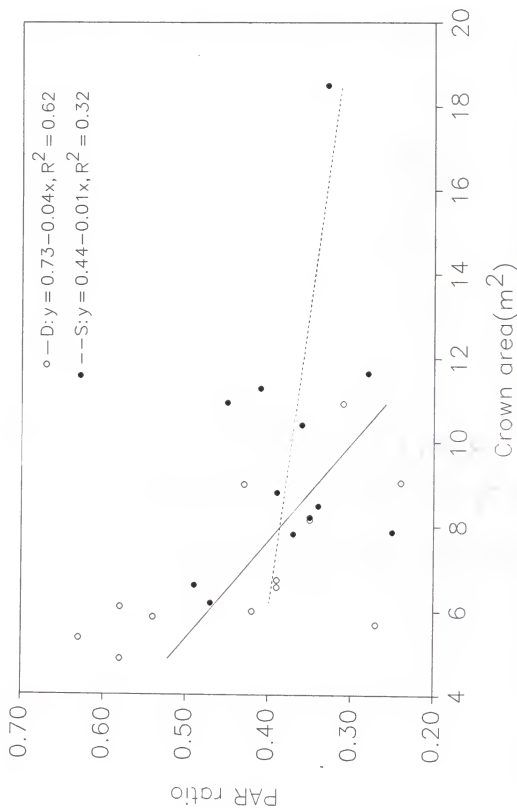


Fig. 7. Regressions of light penetration on crown area of 18-yr-old slash pine at single-row (S) vs double-row (D) configurations ($n = 12$ transects).

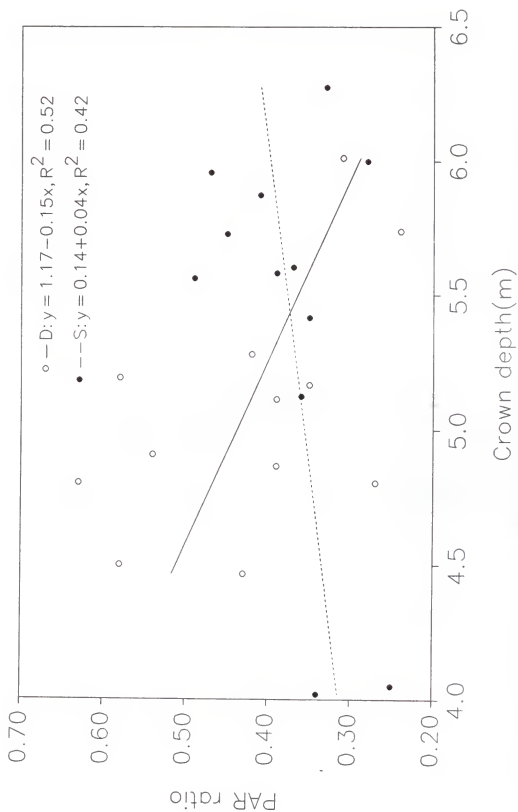


Fig. 8. Regressions of light penetration on crown depth of 18-yr-old slash pine at single-row (S) vs double-row (D) configurations ($n = 12$ transects).

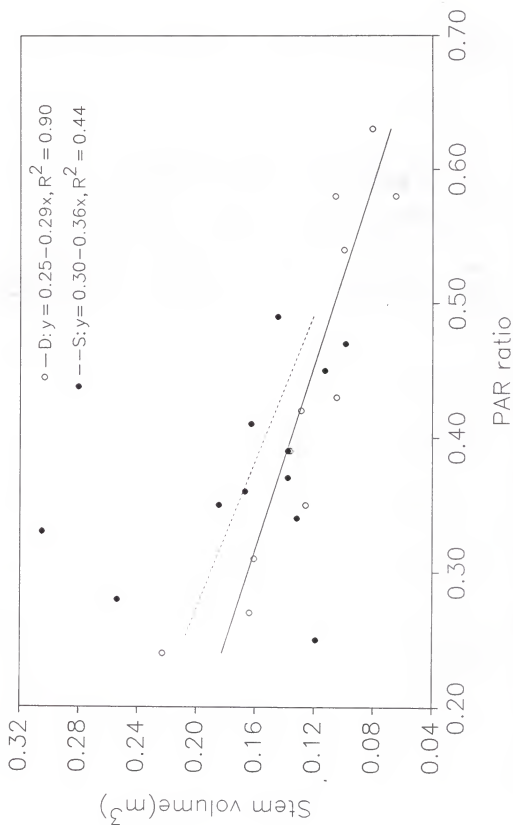


Fig. 9. Regressions of stem volume on light penetration in 18-yr-old slash pine at single-row (S) vs double-row (D) configurations (n = 12 transects).

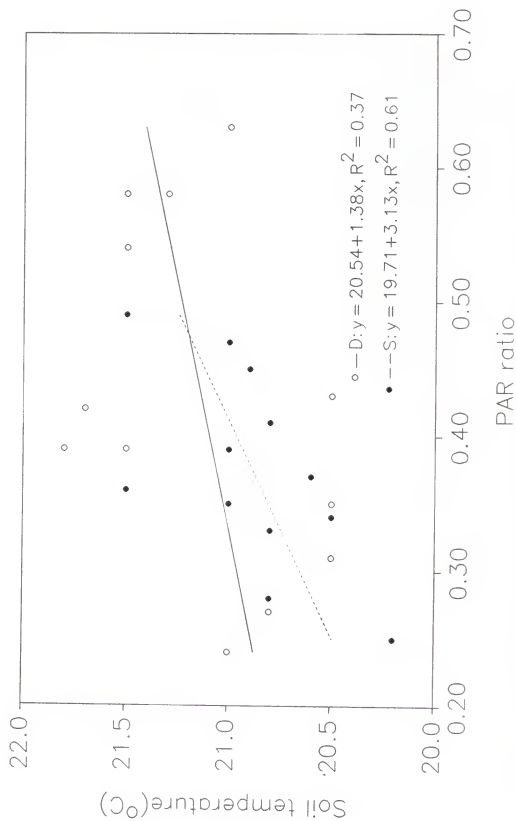


Fig. 10. Regressions of soil temperature on light penetration in 18-yr-old slash pine at single (S) vs double-row (D) configurations ($n = 12$ transects).

Seasonal Variation in Light Penetration and Soil Temperature

There were no significant differences in above-canopy PAR among seasons, with mean values ranging from 1381 $\mu\text{mol}/\text{m}^2/\text{s}$ during the summer to 1080 $\mu\text{mol}/\text{m}^2/\text{s}$ for the fall (Table 10).

Table 10. Mean seasonal variation in light conditions and soil temperature in 18-yr-old slash pine stands, Withlacoochee State Forest.

Seas ^a	aPAR ^b -($\mu\text{mol}/\text{m}^2/\text{s}$)-	bPAR ^c -($\mu\text{mol}/\text{m}^2/\text{s}$)-	PAR ratio (bPAR:aPAR)	LAI ^d	k ^e	Soil temp (°C)
W	1123(184)*	443(220)	0.39(0.19)	4.46	0.49(0.22)	14.7(1.7)
Sp	1359(356)	546(250)	0.39(0.13)	4.26	0.33(0.10)	19.9(1.9)
Su	1381(268)	575(238)	0.43(0.19)	5.21	0.24(0.10)	25.6(1.2)
F	1080(318)	418(237)	0.39(0.18)	6.07	0.27(0.12)	23.8(1.8)

^aWinter, spring, summer and fall, respectively.

^{b,c}Above-canopy and below-canopy photosynthetically active radiation, respectively.

^dLeaf area index (all-sided).

^eLight extinction coefficient.

*Numbers in parentheses denote standard deviations.

Mean below-canopy PAR among configurations also did not vary among seasons, with values ranging from 575 (summer) to 418 (fall) $\mu\text{mol}/\text{m}^2/\text{s}$. Overall, below-canopy PAR tended to increase from a low value in the winter through the spring to reach a maximum in the summer, then to decrease again to a minimum in the fall. Except in the summer, below-canopy PAR tended to be greater for double-row as compared to single-row stands throughout the year (Fig. 11).

There were also no significant differences in light penetration among seasons (annual mean = 0.40 ± 0.17). The difference between double-row (0.42 ± 0.14) and single-row (0.38 ± 0.10) stands was not significant.

Differences in light extinction coefficient (k) were found between winter and spring, between winter and summer, and between spring and fall (k higher for the first of each of the paired seasons) based on non-orthogonal contrasts ($\alpha \leq 0.05$), with values ranging by a factor of two, from 0.49 (winter) to 0.24 (summer). Mean k peaked in the winter, then started dropping through the spring to a minimum in the summer before rising again in the fall. The average for single-row stands was not different than that for double-row stands.

Soil temperature also varied between winter and spring, between winter and summer, and between spring and fall (lower soil temperature for the first season of each pair) based on non-orthogonal contrasts ($\alpha \leq 0.05$), with values ranging from 25.6 (summer) to 14.7 (winter) °C. Mean soil temperature increased from its lowest point in the winter through the spring to a maximum in the summer, then started declining again in the fall. There was no difference in average soil temperature between double-row and single-row stands.

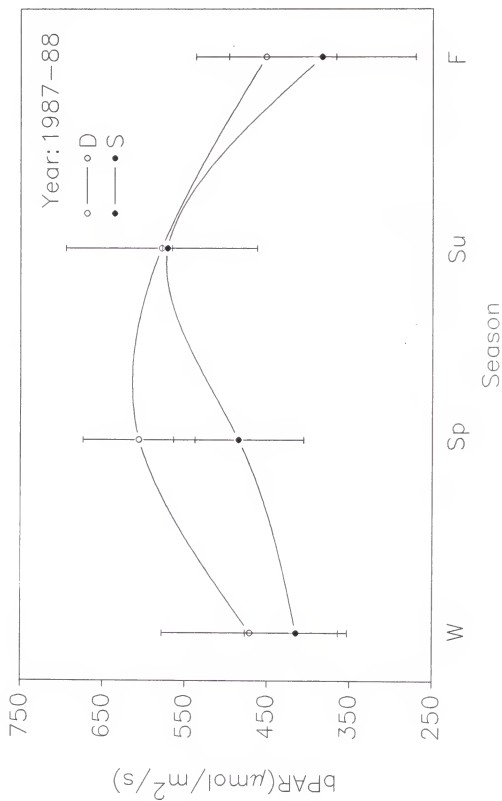


Fig. 11. Seasonal variation in below-canopy PAR in 18-yr-old slash pine at single-row (S) \bar{v}_s double-row (D) configurations.

Diurnal Variation in Light Penetration and Soil Temperature Above-canopy PAR

Mean hourly above-canopy PAR gradually increased from a minimum ($155\text{--}699 \mu\text{mol}/\text{m}^2/\text{s}$) at 0800 hrs to a maximum ($826\text{--}1348 \mu\text{mol}/\text{m}^2/\text{s}$) at 1300 hrs before declining again (Table 11). The relatively low above-canopy PAR readings on diurnal 1 were due to overcast skies during much of the sampling period. The high fluctuations in above-canopy PAR observed between 0800 and 1300 hrs for diurnals 1 and 2 were caused by scattered cloudiness. Also, above-canopy PAR readings had to be stopped earlier in diurnals 3 and 4 because of a rapid onset of cloudy conditions and rain soon after 1400 hrs.

Below-canopy PAR

Mean hourly below-canopy PAR tended to vary in a similar way as above-canopy PAR throughout the day, but in this case the general trend was obscured by a much higher variability in local climatic conditions (cloudiness, wind) at the individual plot level, particularly during diurnal 4. This apparently had an effect on below-canopy PAR readings as compared to the control readings of above-canopy PAR taken at the fixed point in the open. Thus, it tended to rise from a minimum ($43\text{--}64 \mu\text{mol}/\text{m}^2/\text{s}$) at 0800 hrs up to a maximum ($337\text{--}817 \mu\text{mol}/\text{m}^2/\text{s}$) at 1200 hrs and then declined again ($72\text{--}83 \mu\text{mol}/\text{m}^2/\text{s}$) (Table 11). There were significant effects of both configuration ($p \leq 0.05$) and time of day ($p \leq 0.0001$) on below-canopy PAR. Based

Table 11. Mean diurnal variation in light conditions and soil temperature in 19-yr-old slash pine stands at different dates of the year, Withlacoochee State Forest.

Diurnal 1 (30 November 1988)					
Time (hrs)	aPAR ^a --($\mu\text{mol}/\text{m}^2/\text{s}$)--	bPAR ^b	PAR ratio (bPAR:aPAR)	k ^c (LAI ^d =5.19)	Soil temp (°C)
0800	155(41)*	43(14)	0.28(0.09)	1.52(0.37)	17.5(0.5)
0900	541(230)	122(38)	0.23(0.07)	0.86(0.19)	17.7(0.5)
1000	424(162)	226(84)	0.53(0.20)	0.28(0.17)	17.9(0.6)
1100	536(375)	265(145)	0.50(0.27)	0.28(0.20)	18.3(0.6)
1200	555(178)	337(168)	0.61(0.30)	0.19(0.15)	18.6(0.5)
1300	826(302)	295(106)	0.36(0.13)	0.35(0.12)	18.8(0.4)
1400	616(100)	256(103)	0.42(0.17)	0.35(0.17)	19.0(0.5)
1500	545(35)	172(68)	0.32(0.12)	0.55(0.19)	19.0(0.4)
1600	299(120)	83(56)	0.28(0.19)	1.11(0.57)	19.0(0.3)
Diurnal 2 (27 January 1989)					
Time (hrs)	aPAR ^a --($\mu\text{mol}/\text{m}^2/\text{s}$)--	bPAR ^b	PAR ratio (bPAR:aPAR)	k ^c (LAI ^d =4.66)	Soil temp (°C)
0800	463(96)	64(26)	0.14(0.06)	3.62(0.70)	15.1(0.6)
0900	756(83)	265(151)	0.35(0.20)	0.83(0.39)	15.6(0.5)
1000	969(126)	512(357)	0.53(0.37)	0.40(0.33)	16.0(0.7)
1100	1106(372)	667(521)	0.60(0.47)	0.32(0.34)	16.4(0.7)
1200	924(546)	632(613)	0.68(0.66)	0.30(0.36)	16.8(0.5)
1300	1233(500)	706(473)	0.57(0.38)	0.28(0.28)	16.9(0.4)
1400	755(508)	458(357)	0.61(0.47)	0.29(0.29)	17.2(0.5)
1500	1232(284)	212(156)	0.17(0.13)	0.83(0.29)	17.3(0.5)
1600	1119(73)	72(37)	0.06(0.03)	1.65(0.31)	17.2(0.4)

Table 11--continued.

Diurnal 3 (23 June 1989)					
Time (hrs)	aPAR ^a --($\mu\text{mol}/\text{m}^2/\text{s}$)--	bPAR ^b	PAR ratio (bPAR:aPAR)	k ^c (LAI ^d =4.92)	Soil temp (°C)
0800	403(27)	199(65)	0.49(0.16)	0.31(0.14)	23.0(0.1)
0900	453(48)	266(73)	0.59(0.16)	0.17(0.09)	23.8(0.5)
1000	607(59)	426(140)	0.70(0.23)	0.10(0.09)	24.2(0.6)
1100	860(50)	613(200)	0.71(0.23)	0.09(0.08)	24.8(0.7)
1200	1009(128)	817(373)	0.81(0.37)	0.07(0.11)	25.5(0.8)
1300	1348(116)	758(461)	0.56(0.34)	0.16(0.15)	26.2(1.1)
1400	1299(120)	95(57)	0.07(0.04)	0.63(0.18)	25.7(1.0)
Diurnal 4 (26 February 1990)					
Time (hrs)	aPAR ^a --($\mu\text{mol}/\text{m}^2/\text{s}$)--	bPAR ^b	PAR ratio (bPAR:aPAR)	k ^c (LAI ^d =4.06)	Soil temp (°C)
0800	699(120)	410(167)	0.59(0.24)	0.72(0.52)	13.6(0.7)
0900	1041(89)	718(363)	0.69(0.35)	0.31(0.35)	15.6(0.8)
1000	1266(220)	1019(472)	0.81(0.37)	0.16(0.27)	17.2(1.0)
1100	1479(226)	840(541)	0.57(0.37)	0.28(0.25)	19.1(1.4)
1200	1564(416)	513(438)	0.33(0.28)	0.46(0.26)	19.6(1.5)
1300	1486(544)	413(327)	0.28(0.22)	0.47(0.19)	19.4(1.2)
1400	1330(621)	269(93)	0.20(0.07)	0.56(0.11)	19.1(1.2)

^{a,b}Above-canopy and below-canopy photosynthetically active radiation, respectively.

^cLight extinction coefficient.

^dLeaf area index (all-sided).

*Numbers in parentheses denote standard deviations.

on orthogonal contrasts ($p \leq 0.05$), the average value of double-row stands ($D_2 + D_3$) was 65% to 69% greater than of S_1 at most times of day, except for diurnal 4 (Fig. 12 to 15).

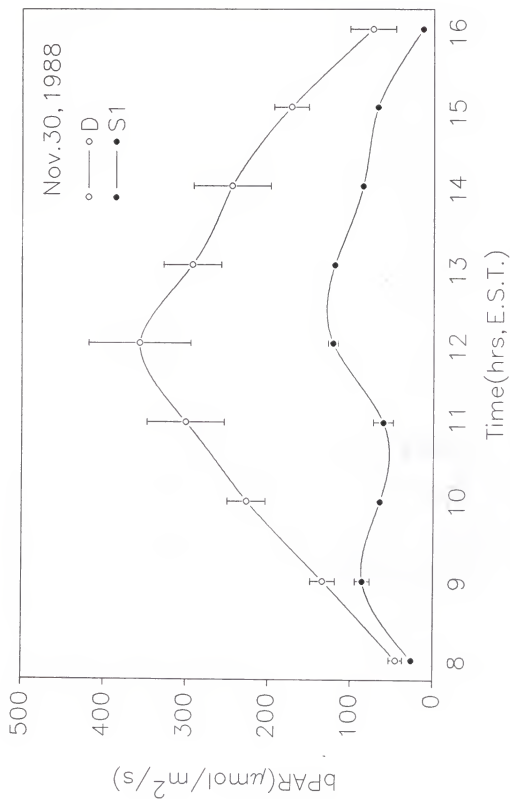


Fig. 12. Diurnal variation in below-canopy PAR in 19-yr-old slash pine at single-row (S₁) vs double-row (D) configurations, November 30, 1988.

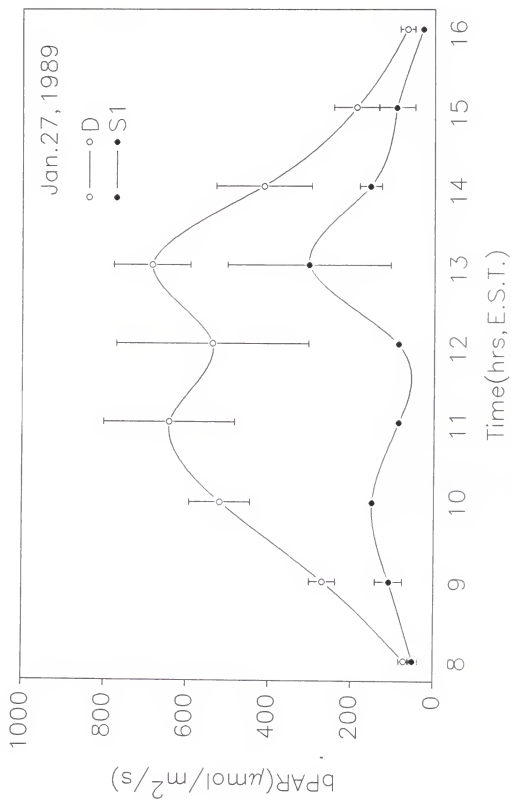


Fig. 13. Diurnal variation in below-canopy PAR in 19-yr-old slash pine at single-row (S_1) vs double-row (D) configurations, January 27, 1989.

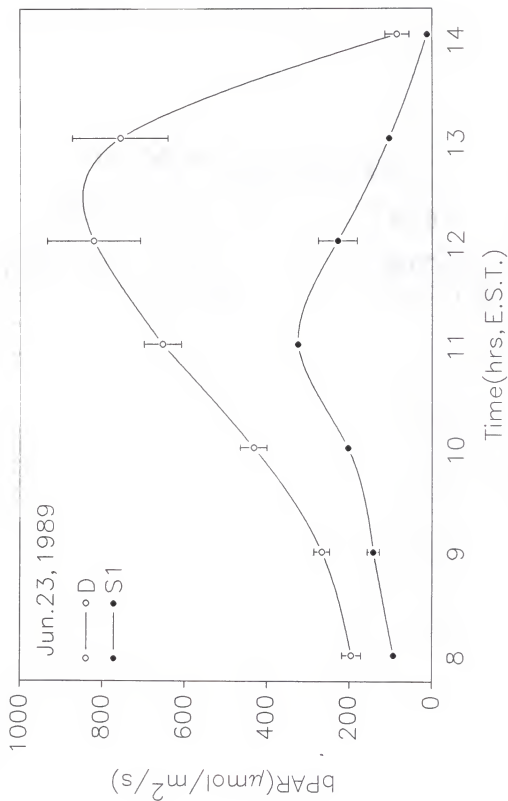


Fig. 14. Diurnal variation in below-canopy PAR in 19-yr-old slash pine at single-row (S₁) vs double-row (D) configurations, June 23, 1989.

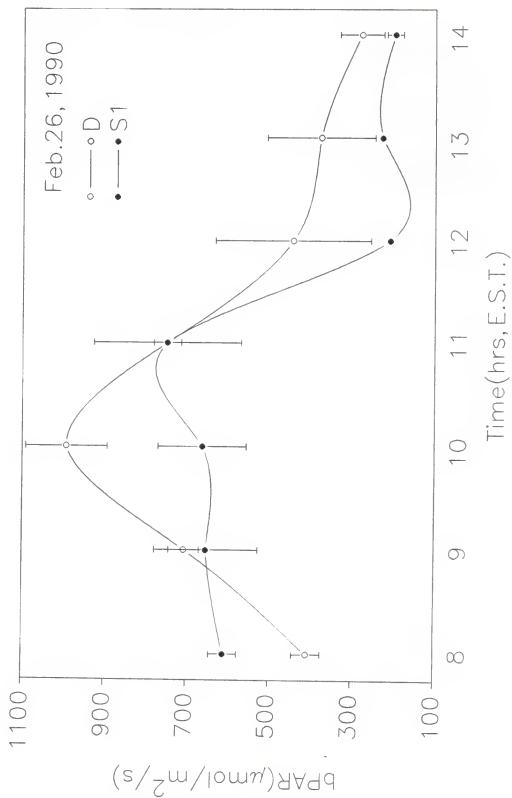


Fig. 15. Diurnal variation in below-canopy PAR in 19-yr-old slash pine at single-row (S1) vs double-row (D) configurations, February 26, 1990.

Light penetration (PAR ratio)

Mean hourly light penetration varied accordingly to both above-canopy and below-canopy PAR, tending to increase from 0800 hrs (0.14-0.59) up to a maximum at 1200 hrs (0.61-0.81) before dropping to a minimum (0.06-0.28) (Table 11). Both configuration and time of day also had a significant effect on light penetration and again, except for diurnal 4, the average for double-row stands was 60% to 69% greater than that for the control throughout the day based on orthogonal contrasts ($p \leq 0.05$) (Fig. 16 to 19).

Light extinction coefficient (k)

Mean hourly light extinction coefficient tended to be inversely proportional to light penetration: first it decreased from a maximum (1.52-3.62) at 0800 hrs down to a minimum (0.07-0.19) at 1200 hrs, and then increased again (1.11-1.65) up to 1600 hrs (Table 11). Except for diurnal 4, both configuration and time of day had a significant effect on k. Mean k for double-row stands was 32% to 55% smaller than that for the control through most of the day based on orthogonal contrasts ($p \leq 0.05$) (Fig. 20 to 23).

Soil temperature

Mean hourly soil temperature tended to increase from a minimum (13.6-23.0 °C) at 0800 hrs up to a maximum (19.0-25.7 °C) at 1400 hrs (Table 11). Time of day had a significant

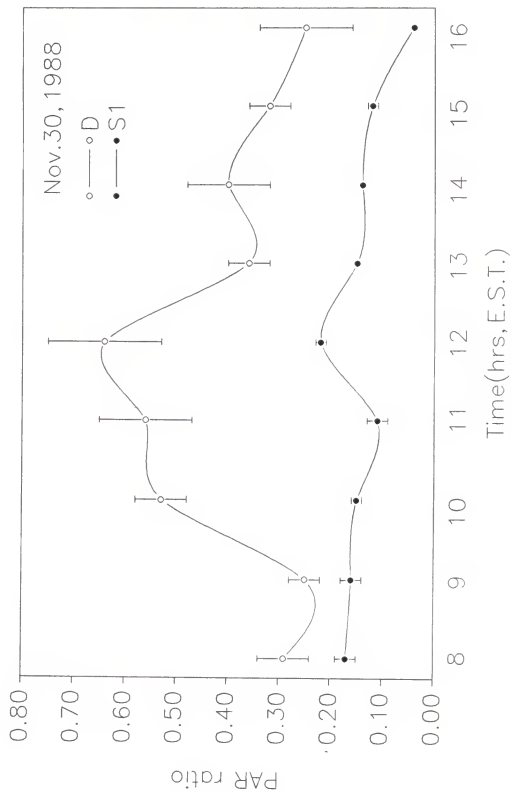


Fig. 16. Diurnal variation in light penetration in 19-yr-old slash pine at single-row (S₁) vs double-row (D) configuration, November 30, 1988.

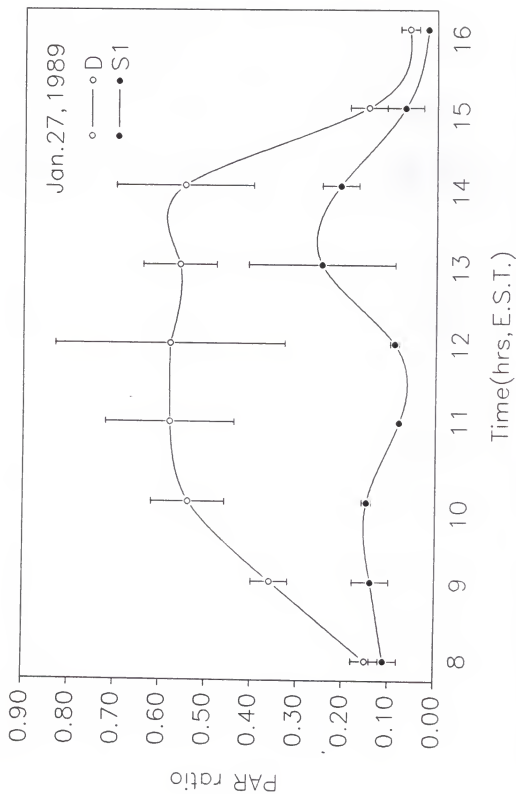


Fig. 17. Diurnal variation in light penetration in 19-yr-old slash pine at single-row (S₁) vs double-row (D) configurations, January 27, 1989.

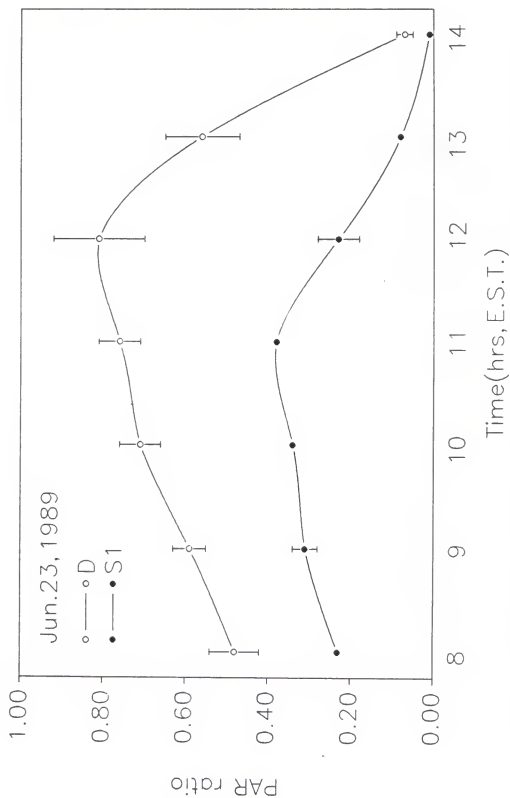


Fig. 18. Diurnal variation in light penetration in 19-yr-old slash pine at single-row (S₁) vs double-row (D) configurations, June 23, 1989.

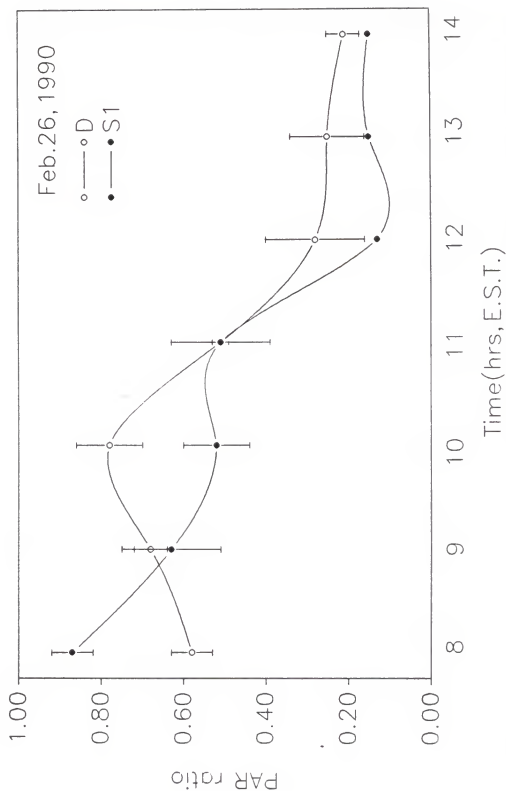


Fig. 19. Diurnal variation in light penetration in 19-yr-old slash pine at single-row (S1) vs double-row (D) configurations, February 26, 1990.

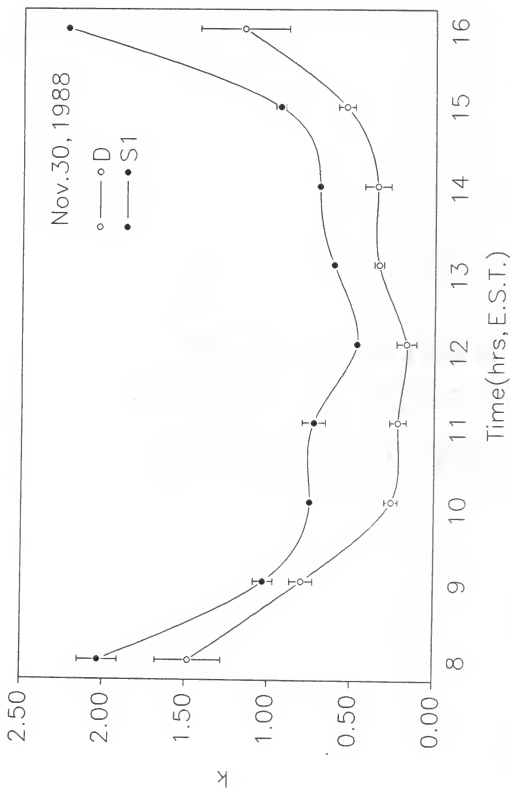


Fig. 20. Diurnal variation in light extinction coefficient in 19-yr-old slash pine at single-row (S1) vs double-row (D) configurations, November 30, 1988.

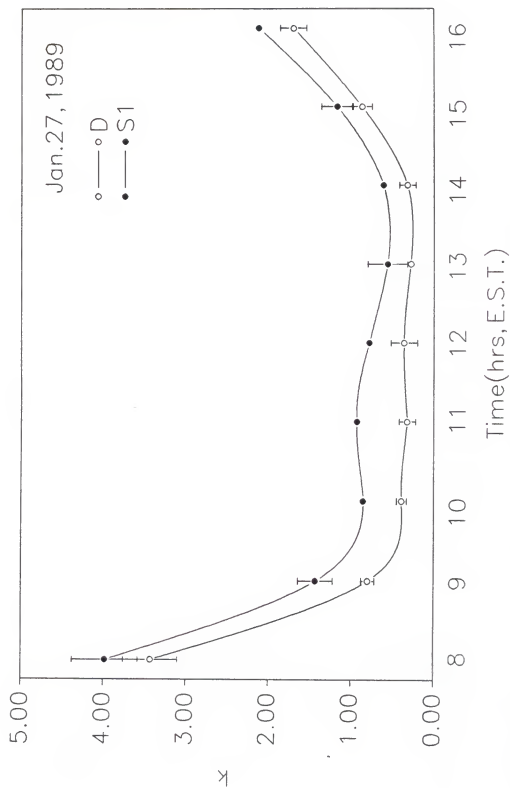


Fig. 21. Diurnal variation in light extinction coefficient in 19-yr-old slash pine at single-row (S1) vs double-row (D) configurations, January 27, 1989.

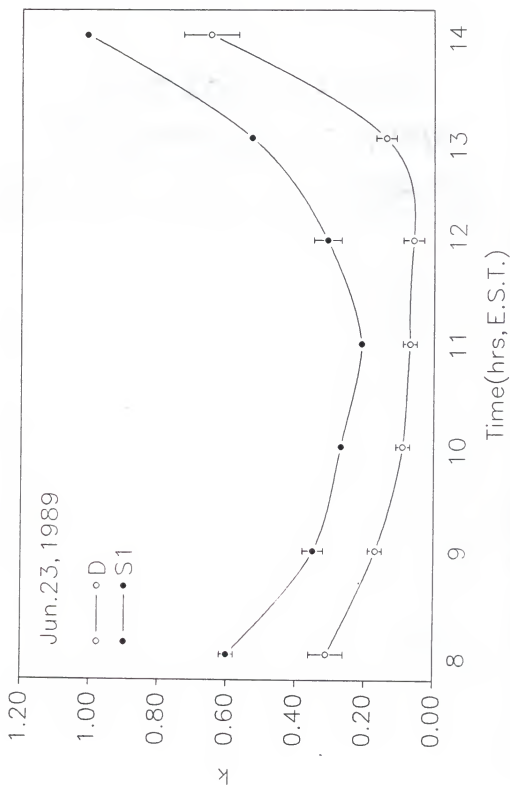


Fig. 22. Diurnal variation in light extinction coefficient in 19-yr-old slash pine at single-row (S1) vs double-row (D) configurations, June 23, 1989.

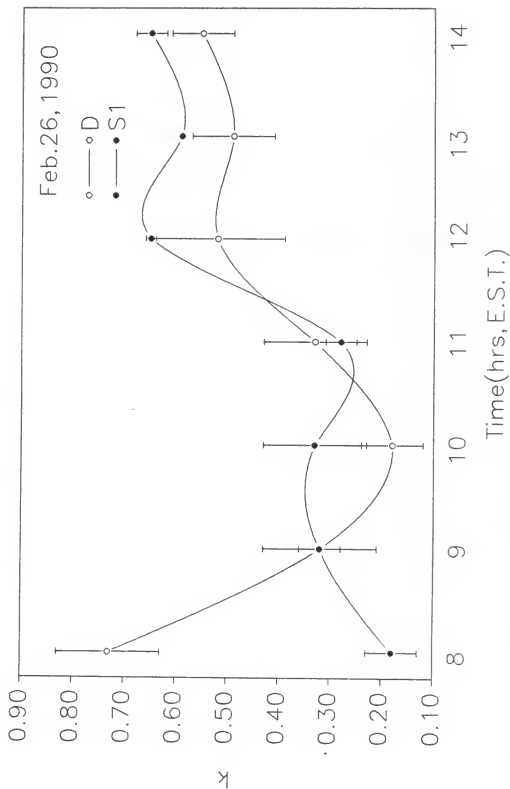


Fig. 23. Diurnal variation in light extinction coefficient in 19-yr-old slash pine at single-row (S1) vs double-row (D) configurations, February 26, 1990.

effect on soil temperature, but there were no differences between double-row stands and the control through most of the day (Fig. 24 to 27).

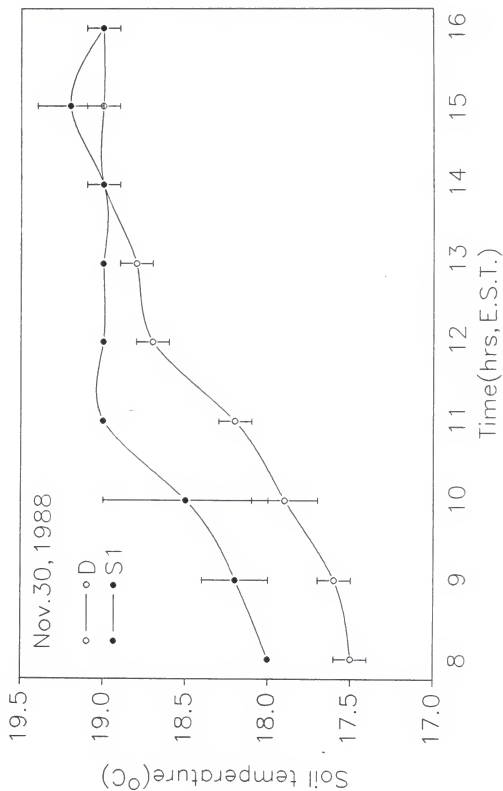


Fig. 24. Diurnal variation in soil temperature in 19-yr-old slash pine at single-row (S₁) vs double-row (D) configurations, November 30, 1988.

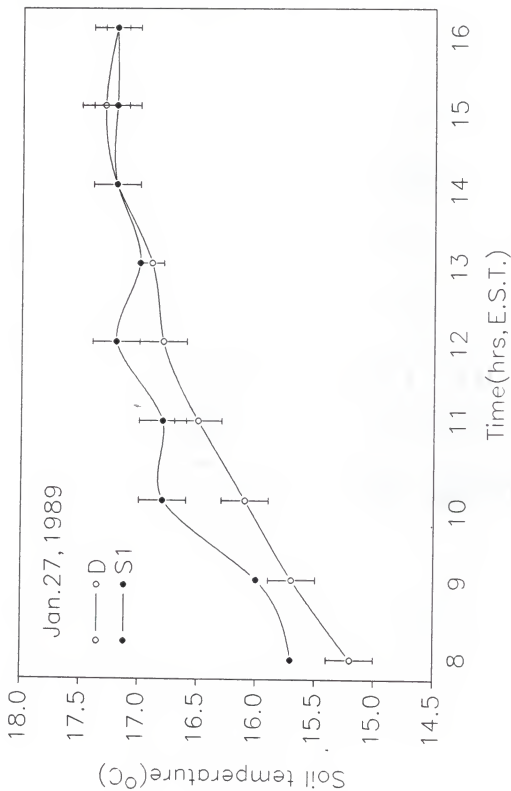


Fig. 25. Diurnal variation in soil temperature in 19-yr-old slash pine at single-row (S₁) vs double-row (D) configurations, January 27, 1989.

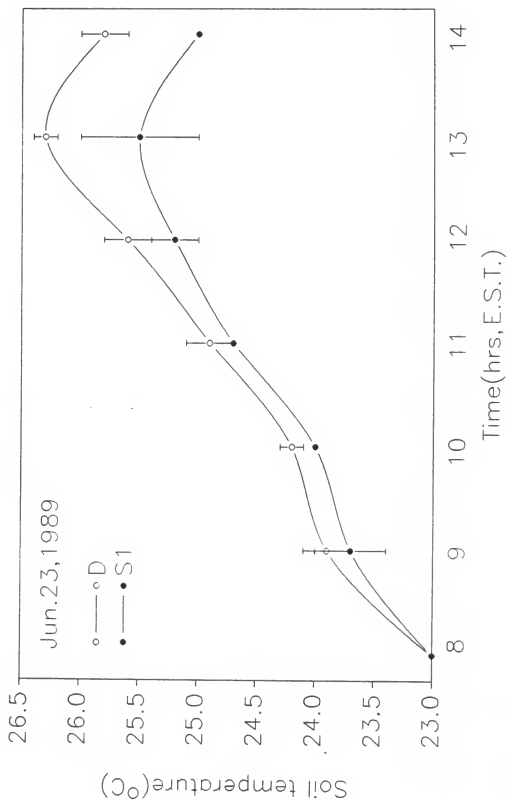


Fig. 26. Diurnal variation in soil temperature in 19-yr-old slash pine at single-row (S₁) vs double-row (D) configurations, June 23, 1989.

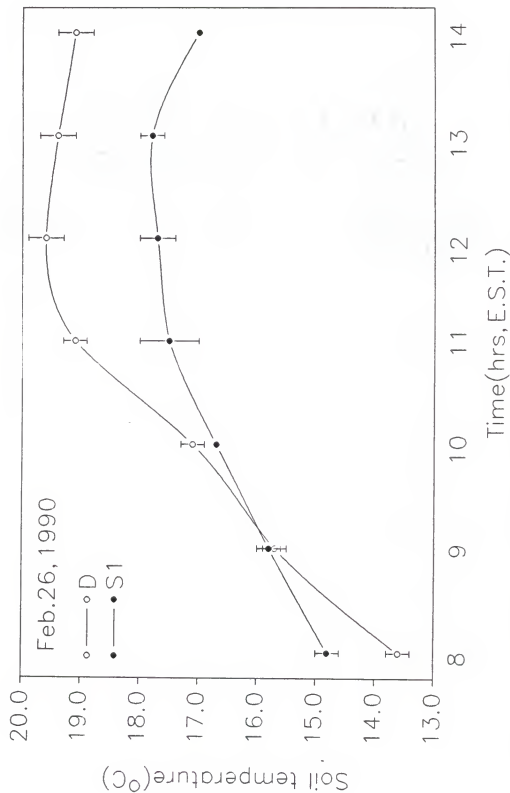


Fig. 27. Diurnal variation in soil temperature in 19-yr-old slash pine at single-row (S₁) vs double-row (D) configurations, February 26, 1990.

CHAPTER 5 DISCUSSION

Canopy Structure and Tree Growth

The combination of wider within-row and closer between-row spacings at a constant stand density in this study favored development of broader tree crowns which would lead to earlier canopy closure. Crown depth and crown ratio, on the other hand, remained relatively constant and were not affected by configuration. In other words, spacing configuration played a more important role in regulating horizontal than vertical expansion of the crown at this particular stand density. Moreover, crown area and crown volume for single-row stands were substantially greater than for double-row stands, suggesting that the packing of trees closer together in the latter case seriously restricted lateral canopy development. The general trend, therefore, was for single-row stands to have broader but not deeper crowns, and for double-row stands to have narrower but not shorter crowns.

Although Gholz and Fisher (1982) documented patterns of LAI and foliar biomass over a 35-yr age sequence of slash pine stands on sites similar to mine, they did not look at canopy structure. A general view of the development of these canopies may be seen in the analysis of McMurtrie et al.

(1986) for radiata pine (*P. radiata*). In the years prior to canopy closure (age 15 yrs), foliage distribution shifted substantially upwards, so that an increase in the height of the live crown was concomitant with a decrease in total canopy depth. As the lower canopy got increasingly shaded, a deficit in the diurnal C balance resulted in higher needle mortality together with lower needle production rates.

Some well-defined differences in stem dimensions also were identified in my study. Whereas tree height did not differ much across configurations, dbh, basal area and stem volume all tended to increase at wider within-row and closer between-row spacings for both single-row and double-row configurations. Apparently, greater stem dimensions were a result of the development of broader crowns and hence increased canopy light interception. Wood yields for the control (S_1) in my study (Table 3) fall closely within the range of those estimated by Bennett and Clutter (1968) for slash pine of similar age, stand density and site index in the Lower Coastal Plains.

If I assume a specific gravity for pine wood of 0.55 g/cm³, stem volume can be converted to biomass increments, which would average 12859 kg/ha/yr for single-row stands and 9845 kg/ha/yr for double-row stands (Table 12). These values are higher than those reported by Gholz et al. (1991) for slash pine stands at similar density in northern Florida. This difference could be attributed to somewhat older age of

the Gholz et al.'s (1991) stands, higher stemwood productivity under non-conventional spacing configurations, or greater soil nutrient availability on my site.

Table 12. Estimated mean annual stemwood biomass increments of slash pine stands between ages 13 and 18 yrs at different spacing configurations, Withlacoochee State Forest.

Spacing config ^a	Stemwood biomass increment (kg/ha/yr)
S ₁	17292
S ₂	13508
S ₃	7777
D ₁	15257
D ₂	7920
D ₃	6358

^aS₁: 2.4x3.6 m, S₂: 1.2x7.2 m, S₃: 0.6x14.4 m, D₁: (1.8x2.4)x7.2 m, D₂: (1.2x2.4)x12.2 m, D₃: (0.6x2.4)x26.6 m.

Increments for unfertilized stands in Gholz et al.'s (1991) study ranged from 2722 to 4547 kg/ha/yr, while those for fertilized stands ranged from 2322 to 8143 kg/ha/yr, indicating the importance of nutrition in affecting tree growth. Dalla-Tea and Jokela (1991) reported an average increase from 3500 for control stands to 8000 kg/ha/yr for fertilized stands of young slash pine planted at high density (1540 trees/ha). They attributed this response to faster canopy development (increased foliar biomass and LAI) and greater light interception on fertilized plots.

The key interactions between nutrient availability and tree production were examined by Vitousek (1982) for a wide variety of forest ecosystems, who concluded that conifers have higher nutrient-use efficiency than broadleaved trees. Gholz et al. (1985) recorded a very high relative nutrient-use efficiency (ANPP+uptake ratio) for slash pine, which increased rapidly with stand age, particularly for P. Yet low rates of mineralization contributed to a nutrient deficit and growth stagnation after 26 yrs on these poor soils. Fisher and Pritchett (1982) obtained a significant response to N fertilization in 6- and 10-yr-old slash pine stands growing on a variety of Lower Coastal Plains soils. Positive responses of slash pine stands to P (Comerford et al. 1987), Mn (Jokela et al. 1991) and application of garbage composted with sewage sludge (Jokela et al. 1990) also have been reported. Further, P fertilization had a beneficial effect on stem form (Jokela et al. 1989). Soil nutrient deficiency and understory competition for nutrients have been identified as the most important factors limiting early growth of slash pine (Swindel et al. 1988; Neary et al. 1990). In young and dense stands, fertilization and weed control each produced a 300% increase in aboveground biomass and LAI, which increased to 450% when both treatments were combined (Colbert et al. 1990). All these studies, therefore, indicate the key role of nutrient status on slash pine growth and the great potential of

improving stand productivity by soil amelioration and weed control.

Linking foliar biomass to area, I found differences only for specific leaf area of new foliage, with the average for double-row stands being slightly larger than for single-row stands. Higher specific leaf areas are generally associated with increased photosynthesis and dry matter production (e.g., Doley 1982). In fact, single-row stands with their larger proportion of new foliage biomass and higher specific leaf area, had greater annual stemwood increments than double-row stands. This supports the relationship between specific leaf weight and annual photosynthetic rate in Larix sp. and Picea abies found by Oren et al. (1986). Likewise, leaf biomass and annual C uptake of Picea were closely correlated. Specific leaf weight, therefore, could be used to adjust leaf biomass values of different crown positions to get reliable estimates of total annual C uptake of the whole canopy.

Apparently, the greater crown volume of single-row stands also contributed to a more effective canopy light absorption and photosynthesis by reducing self-shading through a more evenly distributed foliage. Oren et al. (1987) recorded a similar effect when comparing growth efficiency of high vs low-density stands of ponderosa pine (P. ponderosa). Although my foliar biomass values were higher than reported by Gholz et al. (1991), the specific leaf areas reported here were lower, so that total LAIs were comparable for both studies. On the

other hand, LAI of new foliage in my study was higher and represented a larger proportion of total LAI. This could partially explain the greater stem biomass production found in my study. Leaf area density varied in the same fashion as LAI, but no differences were observed among configurations. The range of values found in my study ($0.93\text{--}1.14\text{ m}^2/\text{m}^3$) is larger than that of Smith and Long (1989) for lodgepole pine (*P. contorta*) stands of various ages and stand densities, probably as a result of the combination of higher LAIs and shorter crown depths in the slash pine stands.

Some research has identified easily measured structural parameters that could be used to reliably predict leaf area and, consequently, biomass production. Grier and Waring (1974) found a linear correlation between leaf area or mass and sapwood basal area (SWBA) for a wide range of western conifers. Gholz and Fisher (1982) observed a similar pattern for slash pine, although the relationship was no longer valid after age 8 yrs (at an average SWBA = $80\text{ cm}^2/\text{tree}$), after which the leaf mass:SWBA ratio became constant. This ratio was slightly larger for single-row ($42\text{ g}/\text{cm}^2$) than for double-row stands ($38\text{ g}/\text{cm}^2$) in my study and reflected the greater canopy development (higher foliar biomass and LAI) in the former. These values (derived from basal area) were somewhat higher than those reported by Gholz and Fisher (1982) and may have contributed to the higher productivity on my site. Also, Pothier et al. (1989) predicted saturated sapwood permeability

at the base of the live crown as a negative exponential function of both age and site quality. This relationship could well be used to "refine" LAI estimates based on the SWBA-leaf mass correlation.

Waring (1980) contended that growth efficiency (GE: stemwood accumulation per unit LAI) declined under stressful conditions and, therefore, that this ratio was a good indicator of site-biomass production relationships under a variety of environments. In my study, GE was lower for single-row (162 g/m^2) than for double-row (180 g/m^2) stands, which allocated more C to stemwood production and, hence, had greater GE than single-row stands. These values were higher than found by Colbert et al.'s (1990) for young slash pine and could also explain the higher productivity in my plots.

The relationships between canopy structure, leaf area and stand productivity have been studied for a number of forest types under different environmental conditions. For instance, Gholz and Fisher (1982) measured maximum all-sided LAI ($6.5 \text{ m}^2/\text{m}^2$) at age 14 yrs in a slash pine chrono-sequence in Florida. ANPP reached a maximum (13 Mg/ha/yr) in mid-rotation and then decreased. In northwestern coniferous forests, Grier and Running (1977) found a strongly negative linear correlation ($R^2 = 0.99$) between all-sided LAI (38 to 43) and a site water balance index. Apparently, this relationship was not affected by species composition along these precipitation and evaporative potential gradients. In a follow-up of this

study, Gholz (1982) identified a close association between biomass, LAI and ANPP, and both a growing season water balance index and minimum winter air temperatures. Both biomass and ANPP increased linearly with LAI up to about a LAI of 30 ha/ha, beyond which ANPP declined. On the other hand, Waring et al. (1981) reported a strongly negative linear relationship between projected LAI and growth expressed as basal area or volume increments of 36-yr-old Douglas-fir (Pseudotsuga menziesii). Net stand increment reached its peak at LAI \approx 6.0 and then started declining at higher leaf areas due to increased mortality.

Gholz (1986) identified several forest types in which a positive relationship existed between LAI and ANPP. Highest ANPP:foliage area ratios corresponded to plantations and young natural stands. Generally, low LAIs combined with modest ANPP rates make pine forests more efficient than other coniferous forests. Nevertheless, in all cases there seemed to be an upper limit to LAI beyond which ANPP starts dropping due to increased self-shading and shading from adjacent trees. By extension, competition for light in my study in the double-row stands, particularly at the closest within-row (but widest between-row) spacings, seriously restricted canopy development and, hence, biomass production.

Light Penetration and Tree Growth

Both above-canopy and below-canopy PAR tended to vary in a similar fashion during the day. Scattered cloudiness and wind contributed to highly variable readings, particularly of below-canopy PAR (Table 11). The total daily above-canopy PAR values (21.6 to 54.7 mol/day) fall within the range reported by Gholz et al. (1991), with the two lowest (on 30 November 1988 and 26 February 1990) corresponding to overcast conditions. Daily light penetration averages (0.39 to 0.56) were higher than those reported by Gholz et al. (1991), but tended to follow a similar seasonal pattern. As with below-canopy PAR, average light penetration of double-row stands was greater than that of the control throughout most of the day.

On the other hand, the estimated Beer-Lambert light extinction coefficient (k) tended to be inversely proportional to light penetration, with the average k value for double-row stands smaller than that for the control through most of the day. The k values seemed primarily determined by season (sun altitude) and time of the day (zenith angle). The highest daily k value (0.95) corresponded to the winter (27 January 1989) when the sun is lowest in the horizon, whereas the lowest (0.22) corresponded to the summer (23 June 1989) when the sun is highest. Using the average seasonal LAI of 5.00, the light extinction coefficient (k) consistently increased at wider within-row and closer between-row spacings. Although there were differences among configurations, the average k

value for single-row stands was not different than that for double-row stands. This trend was the opposite as that of light penetration and could be at least partly associated with changes in zenith angle and time of year. On an annual basis, therefore, spacing configuration did not seem to affect the pattern of light attenuation through the canopy. On a daily basis, higher k values occurred either early in the morning or late in the afternoon at low zenith angles when crown projections reach their maximum and sunlight has to pass through a thicker canopy layer. Shading by adjacent trees rows is therefore very important in determining light penetration and extinction patterns in these stands. Diurnal above-canopy PAR, light penetration and k values had a wider range and variability than seasonal values and, therefore, differences between single-row and double-row stands became more noticeable at the daily rather than seasonal level.

These results support McKelvey's (1990) development of a geometric model of sunlight penetration for slash pine. His study showed only light shading in the top 2 to 3 m of the canopy at any sun angle, mostly due to self-shading. At low sun angles, the lower canopy was heavily shaded by adjacent trees, but this competitive effect became negligible above 60° . Since conic crowns favor the interception of both unobstructed beam and diffuse sky radiation by the lower canopy, exponential light extinction with canopy depth would be only expected at low zenith angles. On the other hand,

Sinclair and Knoerr (1982) found that for a loblolly pine (*P. taeda*) canopy, light extinction increased exponentially with cumulative LAI and depended on sun elevation, too. Light penetration varied with canopy height and time of day, showing a bimodal distribution under mostly direct-beam radiation and a unimodal pattern under predominantly diffuse radiation. In both cases, relative frequency of low transmittance values increased at lower canopy heights.

The above-canopy light conditions were the same for all my stands throughout the year. On the other hand, differences in below-canopy PAR were found among configurations. The overall trend was for below-canopy PAR to increase at closer within-row and wider between-row spacings for both single-row and double-row stands, as a result of the development of narrower, more spatially-restricted canopy cover within rows together with larger gaps between rows allowing more light penetration. In other words, within-row spacing was more crucial in restricting canopy structure, while light penetration was more dependent on between-row spacing. Furthermore, light penetration consistently increased with decreasing crown area (the apparent increase in light penetration with increasing crown depth observed for single-row but not for double-row stands can be disregarded on the grounds of the low fit ($R^2 = 0.42$) of the experimental data).

The above-canopy PAR (47 to 60 mol/day), light penetration (0.39 to 0.43) and light extinction coefficient

(0.24 to 0.49) values were higher and had a narrower range of variability than those of Gholz et al. (1991). This was probably because they represented seasonal instead of monthly averages over a shorter period of the day (1000 to 1500 hrs) when light intensity is highest. Yet they appeared to follow the same general trends. On the other hand, these k values were lower than those reported by Sinclair and Knoerr (1982) for loblolly pine (0.42), and Dalla-Tea and Jokela (1991) for slash and loblolly pines (0.52 to 0.97, on a projected LAI basis). Light penetration did not reflect seasonal fluctuations in LAI in my study, due apparently to the highly aggregated structure of slash pine canopies. This corroborates results of Van Gerwen et al. (1987), Gholz et al. (1991) and McKelvey (1990).

Seasonal variation in canopy light penetration is well documented in the literature. Grace (1987) studied the effect of row orientation on seasonal light interception of radiata pine at a low stand density in New Zealand and found that north-south rows intercepted more sunlight during the summer, but less during the winter, than east-west rows. In a previous study, Jackson and Palmer (1972) reported a similar pattern (at latitude 34°), although in some cases light interception by east-west rows was higher than for north-south rows during the summer. Light interception depended primarily on latitude, and the effect of row orientation decreased with

an increase in the ratio of crop height to distance between crown projections of adjacent rows.

Although tropical deciduous moist forests may represent an extreme case of seasonal changes in canopy structure, their study should lend a better understanding to less seasonally marked patterns of canopy and light penetration changes in low-latitude forests in general. Lee (1989) reported significant seasonal changes in canopy cover and radiation environment of a tropical moist deciduous forest in India. His photosynthetic photon flux density (PPFD) values more closely resembled those of temperate deciduous forests, whose mid-summer values are lower than the post-monsoon tropical forest values, whereas winter and early spring values seem closer to the pre-monsoon readings. Large seasonal changes in LAI in this type of forest are also likely to have a major impact on soil temperature and evaporation. In a similar monsoonal forest, however, Pinker et al. (1980) found no seasonal variation in daily (24-hr) totals of the allwave radiation at the forest floor (75% light penetration). Shortwave radiation (0.3 to 3 μm), on the other hand, exhibited a seasonal pattern, with only 8% of the value at the canopy top reaching the forest floor. Since PAR (0.38 to 0.71 μm) is within this range, a reduction in photosynthesis is likely to occur during the rainy season when intercepted shortwave radiation is at its lowest.

A close association between light interception and tree biomass production has been established for several forest types. Linder (1985) reported a strongly positive linear relationship ($R^2 = 0.99$) between yearly light interception and ANPP of young fertilized stands of eucalyptus (*E. globulus*) growing in Australia. When compared to European stands, annual light interception accounted for most of the differences in ANPP. Likewise, Whitehead (1986) showed that light interception by radiata pine (*P. radiata*) was primarily dependent upon LAI and the presence of gaps in the canopy. Also, aboveground dry matter production increased with canopy light interception, the former determined by leaf area density and the efficiency of conversion.

Based on the values in Table 9, and assuming 12-hr daylight, an average annual PAR interception of 11668 mol/m² (i.e., 2536 MJ, or 60% of incoming PAR) can be derived. This is equivalent to a light use efficiency of 0.10 g/mol PAR or 0.46 g/MJ incident radiation (1 MJ = 4.6 mol, Landsberg 1986) for an average stem biomass increment of 11352 kg/ha/yr. These values are very similar to those reported by Gholz et al. (1991) and Dalla-Tea and Jokela (1991) for biomass increment of fertilized slash pine stands. Annual PAR interception can be estimated at 11174 and 12163 mol/m²/yr (i.e., 57% and 63% of incoming PAR) for double-row and single-row stands, equivalent to light efficiencies of 0.9 and 0.11 g/mol PAR or 0.41 and 0.51 g/MJ incident radiation for stem

biomass increments of 9845 and 12859 kg/ha/yr, respectively, for the two configurations.

Differences in light use efficiency between control and fertilized plots in Gholz et al.'s (1991) study were much larger than those between single-row and double-row stands in my study, suggesting that nutritional status is a more important factor than stand geometry in affecting biomass production of slash pine stands. Therefore, slash pine seems well-adapted to relatively warm and nutrient-deficient sites through low light-use but high nutrient-use efficiencies (Gholz et al. 1991).

Kellomäki et al. (1986) contended that, although stand density ultimately plays a more critical role than crown shape in regulating canopy light absorption, narrow and symmetrical crowns regularly distributed in a dense stand should be more efficient because both gaps and overlap between crowns would be minimized. Crown shape (the ratio of crown depth to crown radius, derived from the values in Table 1) in my study ranged from 3.69 (D_3) to 2.63 (S_1), and tended to consistently increase at closer within-row and wider between-row spacings for both single-row and double-row stands. Average crown shape for double-row stands (3.45) was larger than for single-row stands (3.14), although both values are low compared to those used by Kellomäki et al. (1986) in their simulation study of canopy structure and light interception for coniferous trees. In my plots, light penetration increased

with increasing crown shape ratios (i.e., more conical crowns) for all stands. This somewhat contrasts with Kellomäki et al.'s (1986) findings, although the comparison is only partly valid since in their model stand density varied and crown volume was constant. In addition, they found no significant differences in canopy light interception at low crown shape values, but as these increased narrower crowns tended to be more effective, especially at high latitudes (low sun elevation) and stand densities (Pukkala and Kuuluvainen 1987).

In contrast, Smith and Long (1989) found that stemwood production and growth efficiency declined with increasing canopy depth and, therefore, both went up in stands with predominantly short and compact crowns. Since high stand density is correlated with restricted crown depth, they further suggested that stand productivity should be directly proportional to stand density. Although stand density remained constant in my study, changing "local" density by packing trees closer together within rows and in double rows reduced annual stemwood increments. In contrast, derived growth efficiency (volume increment per tree height increment per unit LAI) of double-row stands ($4.8 \cdot 10^{-4} \text{ m}^3/\text{m}/\text{m}^2$) was somewhat higher compared to single-row ($4.4 \cdot 10^{-4} \text{ m}^3/\text{m}/\text{m}^2$) stands. Since double-row stands in my study tended to develop more compact crowns, this could explain their relatively higher growth efficiency, which is consistent with Smith and Long's (1989) findings. This highlights the potential of non-

conventional spacing configurations for increasing light penetration to the understory while still maintaining moderate wood yields in silvopastoral systems.

Smith and Long (1989) further suggested a link between high stand "vigor" and rapid growth of individual trees with deep full crowns. Indeed, Waring and Pitman (1985) provided evidence of increased resistance of lodgepole pine to mountain pine beetle (Dendroctonus ponderosae Hopkins) attack by increasing growth efficiency of surviving trees after thinning.

Daily soil temperature in my study tended to increase concomitantly with above-canopy PAR and light penetration, but at a somewhat lower rate and, hence, peaking at a later time of day. No difference in average hourly soil temperature was found between single-row and double-row stands. The range and variability of hourly soil temperature values were smaller than seasonal values, so that differences between single-row and double-row stands were relatively small in this case, too.

Canopy Structure, Light Penetration and Overstory-Understory Relationships

Although of great importance, the understory contribution has been traditionally overlooked in forest production studies. Nevertheless, there is now growing interest in this neglected area and more papers in the literature are addressing the complexity of overstory-understory relationships.

In many situations, competition for light seems to be one of the primary factors limiting growth of both understory and overstory species. For instance, Dahlem and Boerner (1987) determined that an increase in light penetration through a canopy gap induced an increase in biomass, rhizome mass and percent of flowering Geranium maculatum. Artificial shading also resulted in increased fruit abortion and decreased time for leaf expansion.

McLaughlin (1978) reported that basal area and canopy opening were significantly correlated to light penetration in a ponderosa pine forest. Nevertheless, most of the variation was primarily dependent on canopy opening, whereas basal area was the poorest estimator of light penetration. He suggested that, in terms of assessing overstory-understory relationships, a close fit of canopy opening with understory cover or production would indicate that competition for light is the main limiting factor to growth.

Long and Turner (1975) reported a decrease in total understory biomass with increasing aboveground tree biomass of Douglas-fir. This decrease was primarily attributed to a decline in the biomass of the dominant understory species, Gaultheria shallon, which was inversely proportional to overstory foliar biomass. At the same time, there was a rise in the diversity of both overstory and understory, partly because of species enrichment, but most of all because of the gradual loss of Douglas-fir dominance at the expense of other

tree species, such as Tsuga heterophylla, as they grew larger over time.

Oren et al. (1987) determined an exponential decrease in GE of ponderosa pine at increasing LAI. The absence of understory favored a more rapid canopy development and higher GE, particularly at low LAIs. Nevertheless, GE stabilized at LAIs above 2.0 independently of understory vegetation.

Gholz and Fisher (1982) found that understory biomass under slash pine plantations peaked at age 5 yrs, then decreased, and rose again after age 26 yrs; it was inversely proportional to tree foliage mass at all ages. Understory ANPP was larger than tree productivity until age 5 yrs and was relatively small after age 8 yrs. After canopy closure, maximum understory total biomass matched that of tree foliage. Also, at age 2 yrs, total system foliage mass (including understory) was already half of the maximum.

The feasibility of promoting forage production for cattle raising under pine forests has been amply studied in the southeastern USA. For instance, slash pine was successfully planted in a dense pasture sod and on well-disked soils with no apparent effect of cultivation or fertilization (Lewis 1985). Forage production decreased linearly as stand basal area increased due to shading (Hart et al. 1970; Lewis 1989; Lewis et al. 1983), whereas fertilization substantially increased yields of improved grasses (Hart et al. 1970; Lewis et al. 1985a). However, grazing increased tree mortality

(Lewis et al. 1985a). Improved pastures have great potential to increase forage yields by supplementing native pine-land three-awn ranges (Lewis and McCormick 1971) and by allowing grazing and hay production when grown under low-density stands (Lewis et al. 1983, 1984). These integrated silvopastoral systems, therefore, seem promising for dual-use management of forest resources in the flatwoods (Lewis et al. 1982).

The planting of trees at non-conventional configurations (e.g., wider spacings and lower densities) would delay or prevent canopy closure, allowing more light penetration to the understory while achieving more of a balance with overstory productivity. Reductions in timber revenues (e.g., from configurations S_3 , D_2 and D_3) could be offset by incorporating some of the pasture management suggested by the research mentioned above. Regulating stand geometry, therefore, could be one of the possible ways to optimize total production potential of these systems by effectively manipulating relative light interception of both overstory and understory components. The results from my study provide some evidence in this direction, but more research is needed involving understory response to overstory spacing configuration and the effects of variable stand density on aboveground and belowground competition. In addition, the decline in growth rates between ages 13 (Lewis et al. 1985b) and 18 yrs (my study) of the closer spaced stands indicates that thinning

after 13 yrs may be useful in order to achieve sustainable wood and forage yield levels over a rotation.

CHAPTER 6 CONCLUSIONS

Three basic hypotheses in this study were tested and basically verified, namely:

1. More crowded trees had smaller crowns, foliar biomasses and leaf areas than more widely spaced trees.

2. As a result, double-row stands had smaller tree dimensions and growth rates than single-row stands.

3. Daily, seasonal and annual light penetration tended to be higher for double-row than for single-row stands. There were no significant differences in soil temperature.

Annual stem biomass increments were reduced in double-row stands, yet their growth and light-use efficiencies were comparable to those of single-row stands. This indicates the potential of non-conventional spacing configurations (single and double rows) for optimizing both wood and forage production in silvopastoral systems, particularly at not extremely close within-row (and extremely wide between-row) spacings.

Despite large seasonal LAI changes in slash pine stands in Florida, there is no clear evidence of proportional changes in annual PAR interception (Gholz et al 1991). Apparently, Lambert-Beer's law is not suitable to describe light

extinction through these irregular canopies and, therefore, more sophisticated models which account for their highly aggregated (clumped) canopy structure (e.g., McKelvey 1990) seem more appropriate. The additional effect of stand configuration could easily be incorporated into such geometric models.

Although not assessed in this study, the key role of nutrient status on slash pine growth is well documented (Comerford et al. 1987; Fisher and Pritchett 1982; Gholz et al. 1991; Jokela et al. 1989; Jokela et al. 1990; Jokela et al. 1991). The species has adapted to poor sites through low light-use but high nutrient-use efficiencies, with nutrient status being a more critical factor than light interception in limiting potential stand productivity. But in an agroforestry context, manipulating light penetration through changes in stand geometry may be more effective and less costly than fertilizing to ensure high understory yields without seriously diminishing tree growth over a rotation.

In addition to spacing configuration, future research priorities should focus on the effect of stand density on canopy structure and light penetration, density management in intermediate-aged stands (13-18 yrs), and overstory-understory interactions in these stands. More attention should be addressed to other bio-ecological factors determining total system biomass accumulation, particularly nutrient availability and water use patterns. Finally, root

development and belowground competition should be also studied in order to complete a picture of tree/understory interactions in these systems.

Extensive research in the past has demonstrated the viability of these systems for cattle raising in Florida (Hart et al. 1970; Lewis 1985, 1989; Lewis and McCormick 1971; Lewis et al. 1982; Lewis et al. 1983, 1984; Lewis et al. 1985a; Lewis et al. 1985b). Newly generated data, therefore, would fill in many of the existing gaps in knowledge and contribute to a better understanding and management of these systems. This goal appears justifiable in view of the dire need for more economically sound and ecologically sustainable alternatives of land use, both in the U.S. and many tropical countries.

APPENDIX A
STEM AND CROWN DIMENSIONS OF SLASH PINE TREES MEASURED FROM
THE NON-DESTRUCTIVE SAMPLING (n = 216).

Tra ^a	Tree	Dbh (cm)	H (m)	Live crown h (m)				Crown radius (m)			
				E	N	W	S	E	N	W	S ^b
22	1	17.2	15.5	8.5	9.5	11.0	10.0	2.8	1.5	1.5	1.1
22	2	12.8	13.5	6.5	8.0	6.5	7.0	2.7	1.1	2.0	1.4
22	3	12.5	13.5	6.0	7.5	6.5	7.5	3.3	1.3	0.9	1.4
22	4	15.8	15.0	8.0	11.0	10.0	11.0	2.2	1.4	1.3	1.2
22	5	13.5	14.0	6.5	9.5	8.5	10.5	2.5	0.7	1.0	0.5
22	6	10.8	14.0	10.0	13.0	10.5	11.5	1.2	0.6	0.4	0.8
22	7	16.8	15.5	9.5	7.0	7.0	9.5	0.3	1.0	2.6	0.7
22	8	10.9	14.0	8.5	8.5	11.5	10.5	1.6	0.4	0.6	1.3
22	9	11.2	9.5	5.0	7.0	4.5	5.0	1.1	1.6	2.6	1.1
22	10	12.3	14.5	9.0	10.0	11.0	10.5	1.2	1.2	1.4	0.6
22	11	^c
22	12	16.1	15.0	9.5	10.0	11.0	8.5	1.0	1.3	2.1	1.0
21	1	9.1	11.0	7.0	8.5	9.0	8.5	2.0	1.0	1.0	1.1
21	2	17.6	16.5	9.5	9.0	11.5	9.5	2.0	1.9	0.5	1.4
21	3	9.8	9.5	5.5	6.0	7.5	6.0	2.1	1.2	0.5	2.2
21	4	11.1	11.5	7.0	9.0	9.5	8.0	2.2	1.9	0.6	1.8
21	5	11.6	13.5	8.0	5.5	10.5	10.0	2.1	1.3	0.4	1.8
21	6	11.8	14.5	8.0	8.0	9.0	9.5	2.1	1.1	0.4	1.0
21	7	8.2	8.5	6.0	5.0	6.5	5.0	0.3	0.5	1.5	1.1
21	8	11.1	10.0	8.0	6.0	6.0	4.5	1.7	1.4	1.1	0.8
21	9	25.0	19.5	9.0	10.5	8.5	9.5	2.0	1.5	3.0	2.0
21	10	9.3	11.5	7.5	4.5	3.5	7.5	1.7	1.2	0.6	1.1
21	11	13.7	15.0	11.0	11.0	7.5	8.5	1.6	1.3	1.6	0.5
21	12	8.5	13.5	9.5	9.0	11.0	8.0	1.6	0.9	0.5	0.5
11	1	16.6	15.5	8.0	9.0	9.0	9.0	1.4	2.4	1.6	1.0
11	2	18.9	16.5	9.0	10.5	10.5	9.5	2.7	1.9	2.4	1.1
11	3	22.0	16.5	9.5	9.5	9.5	8.5	2.1	1.1	2.8	1.2
11	4	14.8	14.5	10.5	10.5	10.0	10.5	1.4	0.4	0.9	1.2
11	5	14.0	14.5	9.5	8.5	7.5	10.0	1.4	0.8	2.0	0.7
11	6	18.0	14.5	9.0	11.0	10.0	19.5	2.3	1.6	1.8	1.6
12	1	13.6	12.5	9.5	10.5	10.0	7.5	1.9	0.5	1.4	1.8
12	2	16.7	12.0	8.5	8.0	9.5	9.5	2.5	1.5	2.0	1.1
12	3	14.6	15.5	11.5	11.0	8.0	12.5	1.0	1.0	1.2	0.6

^aTransects: 61, 62, 121 and 122 = S₁, 11, 12, 101 and 102 = S₂, 51, 52, 71 and 72 = S₃, 81, 82, 111 and 112 = D₁, 41, 42, 91 and 92 = D₂, 21, 22, 31 and 32 = D₃; ^beast, north, west and south directions, respectively; ^cmissing tree.

Tra ^a	Tree	Dbh (cm)	H (m)	Live crown h (m)				Crown radius (m)			
				E	N	W	S	E	N	W	S ^b
12	4	17.3	16.5	10.5	9.0	9.0	9.5	3.2	1.7	2.7	1.0
12	5	20.7	15.0	7.5	9.5	9.5	8.5	3.1	1.8	2.7	1.2
12	6	19.5	15.0	8.5	8.5	8.5	8.5	2.8	1.3	2.3	2.0
32	1	7.2	8.0	5.0	4.0	5.0	4.5	1.0	1.7	0.7	0.3
32	2	8.1	10.0	5.0	4.0	4.0	6.0	1.2	1.3	0.8	0.3
32	3	15.3	14.0	9.5	10.0	10.0	10.0	1.7	0.7	1.4	1.2
32	4	9.0	10.5	5.5	6.0	4.5	5.0	1.6	0.9	0.9	1.1
32	5	10.1	10.5	5.5	8.5	7.5	7.0	2.4	0.8	0.5	0.4
32	6	8.3	8.5	4.5	6.5	7.5	7.5	2.4	1.3	0.6	0.2
32	7	9.8	10.5	7.5	6.5	4.5	6.0	0.6	2.0	3.3	1.6
32	8	8.9	11.5	7.0	8.5	7.5	7.5	1.7	1.4	0.3	0.5
32	9	13.4	14.0	8.5	7.0	7.5	7.5	0.4	0.7	1.9	1.4
32	10	14.0	14.0	12.0	8.5	6.0	9.0	0.7	0.7	2.0	2.0
32	11	15.6	14.5	9.5	9.5	7.5	9.5	1.6	1.5	2.4	0.9
32	12	14.0	13.0	9.5	7.5	6.0	7.5	0.9	1.0	2.1	1.2
31	1	8.0	7.5	5.0	6.0	3.5	5.0	2.2	1.7	0.5	0.6
31	2	11.3	14.0	7.5	11.0	11.0	10.0	2.2	0.5	1.2	0.7
31	3	14.9	13.5	6.5	7.5	8.0	7.5	2.2	1.8	1.4	0.7
31	4	10.2	12.5	4.5	5.5	7.0	5.5	3.2	1.0	0.9	0.8
31	5	13.1	11.5	6.0	6.5	6.5	6.5	3.1	1.3	1.0	1.0
31	6	15.3	14.5	8.5	8.5	9.5	8.5	2.0	1.1	0.8	0.7
31	7	11.0	12.5	8.0	8.5	8.5	8.5	1.1	0.9	1.5	1.1
31	8	14.1	11.5	8.5	7.0	6.5	6.0	0.3	1.9	2.9	1.6
31	9	16.4	15.5	10.5	10.5	10.5	10.5	0.7	0.6	0.7	1.1
31	10	14.2	15.0	11.0	8.5	8.5	10.5	1.0	1.1	2.9	1.0
31	11	8.7	12.5	11.5	6.5	5.5	11.5	0.9	0.9	1.4	0.4
31	12	10.0	11.0	6.5	7.5	5.5	7.5	1.5	1.0	1.3	0.9
42	1	13.2	13.5	8.5	9.5	11.5	10.0	2.1	1.4	1.0	0.7
42	2	15.4	14.0	8.5	8.0	10.0	11.5	2.5	1.4	1.1	0.5
42	3	15.7	16.0	9.0	12.0	13.5	12.0	2.4	1.2	1.1	1.2
42	4	12.1	13.5	10.0	12.0	9.5	9.5	1.5	0.4	0.4	0.8
42	5	17.4	14.5	8.5	9.5	11.0	8.0	2.2	1.2	1.3	1.3
42	6	10.4	12.5	9.0	9.5	9.0	8.0	1.7	1.1	1.3	1.4
42	7	15.5	17.0	10.5	10.5	13.0	10.5	1.4	1.2	1.5	1.2
42	8	16.0	15.5	11.0	11.5	9.0	9.0	1.1	0.9	2.7	1.3
42	9	18.7	16.5	9.0	10.0	9.0	11.0	1.1	1.7	2.2	1.0
42	10	18.1	17.0	13.5	8.0	8.0	13.5	0.8	1.1	3.4	2.0
42	11	12.2	13.0	7.0	7.0	6.5	8.0	1.3	1.1	2.5	0.8
42	12	15.8	15.5	8.5	10.0	8.0	9.0	2.6	1.1	2.0	1.2
41	1	11.3	13.5	9.0	9.0	10.5	9.0	2.3	1.4	0.4	0.8
41	2	14.3	15.5	8.5	8.5	10.0	9.0	2.1	1.0	1.2	1.3
41	3	11.5	14.0	8.5	8.5	10.0	9.5	3.1	1.9	0.7	0.8
41	4	13.2	14.5	8.0	9.0	11.5	9.5	2.8	2.3	0.7	0.6

^aTransects: 61, 62, 121 and 122 = S₁, 11, 12, 101 and 102 = S₂, 51, 52, 71 and 72 = S₃, 81, 82, 111 and 112 = D₁, 41, 42, 91 and 92 = D₂, 21, 22, 31 and 32 = D₃; ^beast, north, west and south directions, respectively; ^cmissing tree.

Tra ^a	Tree	Dbh (cm)	H (m)	Live crown h (m)				Crown radius (m)				S ^b
				E	N	W	S	E	N	W		
41	5	13.2	13.5	9.5	9.5	10.5	9.5	2.2	1.1	1.1	1.1	
41	6	12.3	11.5	7.5	8.0	8.0	7.5	1.8	1.2	1.3	1.0	
41	7	13.0	13.5	9.5	8.0	9.5	9.0	1.4	1.3	2.2	1.3	
41	8	14.9	12.5	8.5	7.0	8.5	8.5	1.5	0.6	3.8	2.6	
41	9	20.0	16.5	9.5	11.0	8.5	8.5	1.9	1.2	2.6	1.3	
41	10	19.4	15.0	10.5	8.0	8.0	10.5	1.5	1.5	2.8	0.7	
41	11	11.9	14.0	8.5	9.5	7.5	8.5	1.7	1.2	2.1	0.8	
41	12	21.0	15.0	8.0	8.0	8.0	9.0	1.7	2.1	3.0	1.3	
51	1	16.6	15.0	8.0	10.5	10.0	9.5	2.2	1.5	2.8	1.1	
51	2	11.9	11.5	6.0	6.0	7.0	8.0	1.9	1.9	2.3	1.3	
51	3	13.7	15.5	8.5	7.5	7.5	11.5	2.1	1.7	0.8	0.6	
51	4	15.7	15.5	7.5	7.5	6.5	10.5	2.8	1.7	2.6	0.8	
51	5	14.5	14.0	8.5	9.0	11.0	9.0	2.1	0.9	1.8	0.7	
51	6	12.4	14.0	8.5	8.5	9.5	8.5	0.3	0.7	2.1	7.0	
52	1	13.7	14.5	6.5	6.5	8.0	10.0	2.5	1.5	2.5	0.6	
52	2	9.9	12.0	8.0	7.0	8.0	7.0	0.5	0.5	2.0	0.6	
52	3	11.7	12.5	7.5	8.0	8.0	10.0	2.4	2.1	0.4	0.3	
52	4	15.0	15.0	9.0	10.0	9.0	11.5	1.6	1.6	2.4	0.6	
52	5	16.2	15.5	8.0	11.5	13.5	9.0	3.7	2.7	0.2	1.2	
52	6	21.9	17.5	9.5	9.5	9.5	9.5	2.8	1.4	2.8	1.9	
62	1	19.2	14.5	7.5	7.0	8.0	8.5	3.5	3.5	1.6	1.8	
62	2	c
62	3	22.3	15.5	11.5	8.0	11.0	12.0	2.8	0.4	1.8	1.3	
62	4	22.7	16.5	9.0	9.0	10.0	11.0	4.0	2.8	2.3	1.4	
62	5	22.2	16.5	9.5	10.5	10.5	10.5	2.5	1.9	2.0	1.6	
62	6	24.9	16.0	8.5	9.5	9.5	9.5	2.8	2.2	2.5	4.7	
61	1	c
61	2	17.8	15.0	11.0	9.0	9.0	10.0	1.5	1.8	1.7	1.3	
61	3	18.8	14.5	9.0	8.0	11.0	10.0	2.4	2.5	2.3	1.5	
61	4	22.4	16.0	8.0	8.0	8.0	8.0	2.3	2.6	2.3	1.5	
61	5	23.1	16.0	9.5	11.5	10.5	9.5	1.4	1.5	1.8	2.1	
61	6	c
72	1	13.9	14.5	11.0	8.0	7.0	9.0	0.9	0.9	2.2	0.8	
72	2	11.0	12.0	7.0	7.0	7.0	8.0	1.9	1.2	2.2	0.7	
72	3	18.0	17.0	10.5	9.5	9.0	11.5	1.5	1.3	2.3	0.6	
72	4	12.4	13.5	7.5	7.5	10.0	10.5	2.5	1.5	0.4	0.3	
72	5	11.4	12.0	9.0	10.5	7.5	9.5	1.3	0.7	1.0	0.6	
72	6	22.8	17.5	8.5	10.0	8.0	9.5	2.8	1.1	2.9	1.9	
71	1	14.3	15.0	9.5	9.5	8.5	11.5	2.3	0.8	1.6	0.8	
71	2	14.2	15.0	8.0	9.5	6.0	7.5	2.9	0.8	2.3	1.1	
71	3	12.8	12.0	8.0	6.0	7.0	6.0	1.4	0.8	2.3	0.6	
71	4	12.7	14.5	5.5	7.5	7.0	7.5	2.0	1.2	1.6	0.8	
71	5	15.5	15.5	9.5	9.5	10.5	9.5	1.7	1.5	1.5	0.7	

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Tra ^a	Tree	Dbh (cm)	H (m)	Live crown h (m)				Crown radius (m)			
				E	N	W	S	E	N	W	S ^b
71	6	10.8	10.0	5.0	5.5	5.5	5.5	0.5	1.2	2.3	0.7
111	1	20.8	16.5	7.5	9.0	9.5	9.0	2.6	2.2	1.5	1.5
111	2	15.0	15.0	7.0	10.5	9.5	9.5	1.6	1.2	1.4	1.1
111	3	14.0	13.5	8.5	8.5	8.5	8.5	2.0	1.8	1.5	1.2
111	4	18.0	14.0	6.5	7.5	10.5	7.5	3.3	2.8	1.6	1.9
111	5	18.8	14.5	7.5	8.5	8.0	8.0	2.6	2.5	2.3	1.4
111	6	16.4	13.5	6.0	9.5	9.5	8.0	3.0	2.0	1.5	1.3
111	7	c
111	8	12.5	13.5	9.5	9.5	7.0	7.0	0.8	2.1	2.0	1.1
111	9	16.6	14.5	9.0	9.0	7.5	7.5	1.2	1.2	2.2	1.5
111	10	13.1	13.5	9.0	7.0	7.0	9.0	1.0	1.7	2.1	1.4
111	11	c
111	12	21.0	15.5	9.0	8.5	8.5	9.0	1.5	1.7	3.0	2.9
112	1	16.4	13.5	8.5	7.0	9.0	8.0	2.2	2.0	1.7	1.1
112	2	14.0	13.5	8.5	9.0	10.5	8.0	2.0	1.2	1.2	1.8
112	3	11.7	9.5	4.5	5.5	5.5	4.5	2.0	2.2	1.3	1.6
112	4	c
112	5	13.0	11.5	8.0	8.0	8.5	8.0	1.6	1.4	0.9	1.1
112	6	14.3	10.5	7.5	7.5	8.0	6.0	1.6	2.1	1.1	1.6
112	7	13.7	11.0	7.0	7.5	6.0	6.5	1.4	1.3	1.8	1.8
112	8	14.6	12.5	5.5	9.0	7.0	8.0	1.4	1.3	2.3	1.6
112	9	18.5	13.0	7.0	8.0	7.0	7.0	1.4	1.9	2.6	2.8
112	10	15.9	13.5	8.0	7.5	10.0	10.0	2.1	2.4	1.9	1.3
112	11	11.1	10.0	6.5	6.5	6.5	7.0	1.4	1.4	1.7	1.3
112	12	17.7	13.5	8.0	9.0	9.0	8.0	1.4	1.9	1.9	1.7
121	1	15.2	13.5	9.5	9.5	8.5	9.5	1.4	1.5	1.3	1.2
121	2	11.9	8.5	8.5	8.5	9.0	8.5	1.4	1.3	1.5	0.8
121	3	14.7	13.5	9.5	9.5	10.0	10.0	1.5	1.4	1.2	0.7
121	4	19.7	14.5	9.0	9.0	9.0	9.0	2.6	2.4	1.9	1.5
121	5	18.1	14.0	8.5	8.5	8.5	8.5	2.3	1.2	1.8	1.7
121	6	15.2	13.5	7.5	8.5	8.5	8.5	2.5	1.7	2.2	1.5
122	1	17.9	14.0	8.5	6.5	8.0	8.5	1.6	2.3	1.9	1.6
122	2	15.6	8.0	8.0	8.0	7.0	8.5	1.5	2.1	1.4	1.4
122	3	14.3	14.5	8.5	9.5	10.0	9.5	1.3	1.3	1.4	1.2
122	4	19.1	13.0	9.0	7.5	8.5	8.0	1.8	1.4	1.8	2.4
122	5	10.6	10.5	6.5	7.0	6.5	5.5	1.2	1.4	0.8	1.4
122	6	c
102	1	15.7	12.5	7.5	7.5	7.5	7.5	2.2	2.2	2.0	0.8
102	2	17.9	17.0	9.0	8.0	9.5	9.5	2.3	2.0	2.2	1.3
102	3	18.2	13.5	8.0	7.5	8.0	7.5	2.2	1.5	2.3	2.9
102	4	c
102	5	16.1	14.0	9.5	9.5	8.5	8.5	1.9	1.2	1.7	1.2
102	6	17.0	15.5	9.0	9.5	9.0	12.0	2.7	1.3	1.8	1.9

^aTransects: 61, 62, 121 and 122 = S₁, 11, 12, 101 and 102 = S₂, 51, 52, 71 and 72 = S₃, 81, 82, 111 and 112 = D₁, 41, 42, 91 and 92 = D₂, 21, 22, 31 and 32 = D₃; ^beast, north, west and south directions, respectively; ^cmissing tree.

Tra ^a	Tree	Dbh (cm)	H (m)	Live crown h (m)				Crown radius (m)			
				E	N	W	S	E	N	W	S ^b
101	1	19.9	16.0	8.5	9.5	8.5	9.5	2.8	2.0	1.5	1.5
101	2	19.1	15.5	9.0	10.0	10.0	10.0	2.2	1.5	2.4	1.4
101	3	12.7	14.0	8.5	9.0	10.5	9.0	2.1	1.2	0.7	0.9
101	4	13.1	14.0	9.0	10.5	9.0	9.0	1.6	0.9	1.4	1.2
101	5	9.3	11.5	5.5	6.5	7.0	7.0	1.5	1.6	1.5	0.7
101	6	16.0	15.0	8.5	7.5	8.5	9.5	2.0	2.0	1.9	0.7
92	1	21.7	15.5	7.5	7.0	9.5	9.5	2.9	2.7	1.6	1.4
92	2	14.8	14.5	8.5	11.0	11.5	9.0	2.8	0.8	0.5	1.1
92	3	13.1	14.5	10.0	10.0	10.5	10.5	1.7	1.1	0.7	0.5
92	4	17.7	14.5	9.5	9.0	9.5	9.5	3.1	1.2	1.1	1.8
92	5	13.1	13.0	9.5	11.0	9.5	8.0	2.8	0.5	0.8	1.8
92	6	12.1	13.5	8.0	9.5	10.5	10.0	2.2	1.2	0.8	0.9
92	7	9.9	11.5	7.5	7.5	8.0	7.5	1.2	1.0	1.6	0.9
92	8	14.5	15.5	10.5	11.0	10.0	11.5	1.6	0.8	1.4	1.0
92	9	19.4	16.5	11.0	10.5	8.0	10.0	1.8	1.4	3.4	1.2
92	10	15.6	15.5	12.0	10.5	10.5	9.0	1.1	0.9	1.8	0.4
92	11	13.2	15.0	13.5	11.0	9.0	7.5	0.6	1.2	2.3	0.8
92	12	c
91	1	14.9	14.0	8.5	9.0	10.0	8.0	2.5	1.5	0.8	0.9
91	2	15.0	15.5	8.5	10.0	10.5	10.5	2.8	0.9	0.9	1.2
91	3	10.4	12.5	8.5	8.5	9.5	9.0	1.6	0.7	0.9	0.6
91	4	13.6	11.5	7.5	7.0	8.0	8.0	2.2	1.2	1.0	1.0
91	5	17.7	16.5	11.5	9.0	10.5	7.5	1.8	1.2	1.5	1.3
91	6	12.7	11.0	6.5	8.0	7.0	6.0	2.5	0.9	1.6	1.5
91	7	11.6	14.5	10.0	10.0	11.5	11.5	1.1	0.6	0.5	0.6
91	8	16.3	16.5	10.0	11.0	9.0	9.0	1.6	1.2	1.9	1.1
91	9	12.7	15.0	9.5	9.0	9.0	9.0	1.0	1.2	1.9	0.6
91	10	8.2	12.5	9.0	7.5	8.0	9.5	0.6	0.5	2.1	0.8
91	11	16.4	16.5	11.5	11.5	9.5	9.5	1.2	0.6	1.7	1.4
91	12	22.6	17.5	11.0	8.0	9.5	10.5	2.4	2.8	2.6	1.0
82	1	20.8	14.5	10.5	8.5	12.0	9.5	3.1	2.1	0.9	1.2
82	2	16.0	14.5	8.5	10.0	9.0	9.0	3.2	1.0	1.1	1.8
82	3	19.3	13.5	9.5	7.5	10.0	9.0	2.0	1.6	1.3	1.6
82	4	17.7	14.5	9.0	10.5	10.5	9.0	1.8	0.9	1.3	1.1
82	5	15.9	13.0	7.0	6.5	9.5	7.5	3.0	1.5	0.9	1.0
82	6	23.6	14.0	8.0	8.0	10.0	8.0	3.1	1.7	1.3	2.0
82	7	22.0	16.0	13.5	8.0	9.0	9.0	1.7	1.6	2.6	1.8
82	8	16.5	15.5	9.5	10.5	9.5	11.5	1.2	1.0	1.6	0.9
82	9	23.3	17.5	11.0	12.0	7.5	10.5	1.3	1.5	3.6	1.4
82	10	18.2	17.5	13.0	9.5	9.5	9.5	1.0	1.8	2.8	0.7
82	11	15.4	17.0	12.5	12.0	11.5	13.0	1.5	1.2	1.7	0.6
82	12	21.0	17.0	10.0	8.0	8.0	8.0	1.9	1.2	3.4	1.7

^aTransects: 61, 62, 121 and 122 = S₁, 11, 12, 101 and 102 = S₂, 51, 52, 71 and 72 = S₃, 81, 82, 111 and 112 = D₁, 41, 42, 91 and 92 = D₂, 21, 22, 31 and 32 = D₃; ^beast, north, west and south directions, respectively; ^cmissing tree.

Tra ^a	Tree	Dbh (cm)	H (m)	Live crown h (m)				Crown radius (m)			
				E	N	W	S	E	N	W	S ^b
81	1	15.2	14.5	12.0	10.5	11.5	10.5	1.5	0.9	1.1	0.9
81	2	16.1	14.0	10.5	9.0	10.5	10.5	2.3	2.0	1.2	0.9
81	3	13.7	12.5	8.5	10.5	9.0	8.5	2.2	1.1	0.7	1.9
81	4	17.0	15.5	8.0	8.5	9.5	10.0	2.3	1.4	1.5	1.3
81	5	16.3	13.5	7.5	8.5	8.5	8.5	2.3	1.3	1.2	1.4
81	6	14.6	14.0	9.5	8.0	8.0	10.0	1.7	1.2	1.3	0.8
81	7	19.4	18.0	13.5	11.0	11.5	10.5	1.3	1.1	1.4	1.3
81	8	15.8	15.5	11.5	10.5	11.5	11.5	1.0	1.0	1.8	0.9
81	9	15.3	16.0	11.0	10.5	10.0	11.0	1.1	1.0	1.7	0.9
81	10	20.9	17.5	15.0	10.5	9.5	10.5	1.3	1.2	2.4	1.0
81	11	17.2	15.5	12.5	11.5	10.5	10.5	1.1	1.1	1.3	0.8
81	12	16.6	15.0	13.5	10.5	10.5	10.5	1.0	1.4	1.7	0.7

^aTransects: 61, 62, 121 and 122 = S₁, 11, 12, 101 and 102 = S₂, 51, 52, 71 and 72 = S₃, 81, 82, 111 and 112 = D₁, 41, 42, 91 and 92 = D₂, 21, 22, 31 and 32 = D₃; ^beast, north, west and south directions, respectively; ^cmissing tree.

APPENDIX B
STEM AND CROWN DIMENSIONS OF SLASH PINE TREES MEASURED FROM
THE DESTRUCTIVE SAMPLING (n = 40).

Tre ^a	Dbh (cm)	H (m)	Live crown h (m)				Crown radius (m)			
			E	N	W	S	E	N	W	S ^b
20	15.5	14.0	9.8	8.9	7.5	11.0	1.6	0.8	2.7	1.0
21	16.8	16.5	7.0	6.2	6.0	9.5	2.5	2.0	2.2	0.5
22	16.9	15.2	9.2	9.2	7.2	6.3	0.8	0.6	2.9	2.1
23	14.8	16.7	11.3	12.3	10.2	9.0	1.2	0.2	2.0	1.4
24	14.0	14.2	11.2	11.2	11.7	9.5	1.6	1.0	1.0	1.5
25	12.3	14.5	7.2	9.3	13.5	12.8	2.9	1.2	0.3	0.4
26	12.5	13.7	7.3	9.0	9.2	9.5	2.4	0.9	1.3	1.0
27	15.1	14.7	8.3	10.3	10.2	9.2	1.7	0.9	1.4	1.0
28	14.4	15.0	11.0	10.2	9.3	10.2	1.0	1.5	2.3	0.5
29	17.6	16.0	9.5	13.3	13.3	10.7	2.7	0.5	0.7	0.4
60	18.3	15.5	8.0	8.2	8.0	7.7	3.2	1.9	1.7	2.9
61	16.4	15.3	9.7	10.7	7.8	9.8	1.5	1.7	2.4	1.4
62	20.2	13.0	7.8	7.5	7.8	8.3	1.9	2.2	2.1	1.4
63	17.3	17.5	11.0	11.0	11.5	9.5	0.8	1.4	2.1	1.4
64	23.0	16.0	10.2	9.5	9.2	8.5	1.6	1.4	2.6	2.7
65	21.2	19.5	10.0	12.2	12.0	10.7	2.8	1.7	1.1	2.5
66	22.6	18.7	10.2	10.2	10.2	10.2	2.1	1.9	2.1	2.7
67	21.3	17.5	11.7	11.7	10.2	10.2	1.7	2.5	1.4	2.6
68	23.5	18.5	10.7	10.7	12.0	12.0	2.5	3.1	2.6	3.0
69	24.3	18.5	9.3	9.3	9.3	9.3	2.4	2.8	2.6	2.1
70	14.5	16.5	12.5	13.0	9.0	12.5	1.6	0.8	2.1	0.7
71	20.5	18.0	10.5	10.7	9.5	12.0	2.5	1.0	2.1	1.8
72	14.3	15.5	9.0	14.2	11.3	11.3	2.4	0.8	2.1	0.6
73	16.2	17.5	10.3	12.7	11.5	11.3	2.5	1.3	2.5	1.4
74	19.4	16.3	7.8	8.7	6.5	8.9	3.6	1.9	4.0	1.2
75	17.2	17.7	8.8	10.1	11.5	11.5	2.8	1.3	1.8	1.2
76	16.0	17.0	10.0	11.1	9.4	10.9	2.3	0.5	1.4	1.3
77	18.2	17.3	10.0	10.0	8.3	11.5	2.5	0.7	1.8	0.8
78	17.9	15.7	8.7	8.7	8.7	8.7	3.3	0.8	3.2	1.2
79	19.4	16.5	12.8	11.7	8.5	10.7	2.6	1.1	2.9	0.5
110	16.4	14.0	6.0	6.0	6.0	8.0	2.5	2.1	1.9	2.2
111	16.8	15.2	8.6	8.9	9.3	9.0	1.9	1.5	1.7	1.6
112	16.9	15.3	8.3	9.5	10.0	9.7	2.6	2.2	1.9	1.3
113	17.4	16.0	10.8	9.8	10.7	10.7	1.4	1.6	2.0	1.0
114	16.3	14.0	7.7	7.7	9.9	8.3	2.5	0.7	1.1	1.6
115	18.7	16.0	8.5	8.5	8.5	8.5	1.4	1.3	2.7	2.3

Tree ^a	Dbh (cm)	H (m)	Live crown h (m)				Crown radius (m)			
			E	N	W	S	E	N	W	S ^b
116	17.8	15.3	8.0	9.0	9.0	8.9	2.2	1.5	1.4	1.3
117	14.3	15.0	10.5	12.3	10.5	8.5	0.7	0.5	1.3	2.0
118	17.3	16.5	8.3	9.8	11.0	10.0	2.8	1.0	1.3	1.0
119	16.4	14.5	8.0	7.3	8.0	8.0	1.1	2.5	1.9	1.9

^aTree: 60-69 = S₁, 70-79 = S₃, 110-119 = D₁, 20-29 = D₃; ^beast, north, west and south directions, respectively.

APPENDIX C
FOLIAR BIOMASS OF SLASH PINE TREES MEASURED FROM THE
DESTRUCTIVE SAMPLING (n = 40).

Tre ^a	Total	Sample	Of ^b	Nf ^c	Ot ^d	Nt ^e	Lf ^f	Lt ^g
	(fresh wt, g)		-----	(dry weight, g)	-----			
20	12600	1800	129	301	83	61	244	113
21	23500	2800	243	491	170	82	160	140
22	20900	3100	355	697	205	92	425	290
23	15000	1800	202	248	152	69	277	205
24	10600	1400	226	265	77	40	612	347
25	10200	1100	238	282	69	37	148	60
26	11700	1800	296	415	89	43	98	51
27	15000	1800	263	436	81	74	242	198
28	16200	1800	312	487	157	76	224	138
29	22200	2300	207	344	98	70	106	54
60	31100	3600	604	666	307	131	721	420
61	17700	2400	166	232	70	65	159	116
62	31700	3700	466	573	152	92	194	164
63	17100	2500	234	623	73	87	224	288
64	29100	3500	213	889	149	156	264	296
65	31600	3800	413	600	231	94	431	469
66	32100	3400	298	648	169	85	353	486
67	33900	3600	536	802	252	200	265	245
68	36500	4100	327	790	197	200	233	271
69	57600	6300	546	1195	186	178	348	582
70	8100	1700	92	660	76	75	314	286
71	41200	4100	672	1114	284	170	640	669
72	11700	1600	119	352	92	84	242	128
73	21300	2400	318	398	202	121	203	145
74	30300	3300	258	576	140	103	159	148
75	23700	2900	466	724	213	139	401	260
76	18600	2400	349	560	177	102	316	167
77	22600	3200	292	683	155	83	376	314
78	20500	2900	240	662	108	89	449	435
79	28200	3000	338	836	189	155	310	226
110	28200	2900	339	549	93	50	499	589
111	46900	4800	585	821	411	101	340	708
112	27000	2800	438	566	198	140	404	367
113	15200	1900	321	419	76	52	286	232
114	13200	2000	136	315	79	59	246	190
115	35400	3600	537	613	128	74	576	322

Tree	Total	Sample	Of ^a	Nf ^b	Ot ^c	Nt ^d	Lf ^e	Lt ^f
	fresh wt, g		-----dry weight, g-----					
116	22900	2500	301	512	106	99	408	355
117	12800	1900	148	333	84	47	216	179
118	20500	2400	502	411	178	62	398	347
119	16900	2400	244	478	101	79	479	570

^aTrees: 60-69 = S₁, 70-79 = S₃, 110-119 = D₁, 20-29 = D₃; ^bold foliage; ^cnew foliage; ^dold twigs; ^enew twigs; ^fleader's foliage; ^gleader's twigs.

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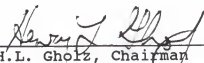
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BIOGRAPHICAL SKETCH

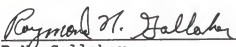
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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.




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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



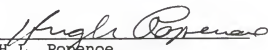
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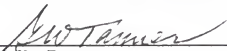
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